University of Alberta

FORAGING BEHAVIOUR AND POPULATION DYNAMICS OF COLLARED PIKAS, *OCHOTONA COLLARIS*

by

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Abstract

I examined the foraging behaviour and population dynamics of a small alpine herbivore, the collared pika (*Ochotona collaris*: Lagomorpha), in the Ruby Range of southwest Yukon. Using a combination of manipulative and mensurative experiments, combined with matrix population models, I explored 1) how pikas selected and cached vegetation ('haying') for winter consumption, 2) the impact of haying behaviour on over-winter survival, and 3) the drivers and consequences of observed population dynamics via climate influences on spring snowmelt patterns and forage availability. Experiments showed haying pikas were extremely sensitive to predation risk when venturing into meadows, but were consistent in their forage selection irrespective of perceived risk. Crude protein and water content levels interacted to influence forage selection, although this effect varied among plant species and suggested pikas made both inter- and intra-specific decisions while haying. Simulations of haypile mass based on video-surveillance data indicated pikas collected ≥5.9 months of vegetation which was sufficient to survive most winters at this site. The annual onset of haying had a large, but inconsistent, effect on over-winter survival for all age and sex classes further implicating haying behaviour as an important influence on population dynamics. Analysis of twelve years of census data from three subpopulations using life table response experiments indicated the observed population declines were due largely to variation in adult female survival and fertility. Adult survival, but not fertility, was strongly correlated to large-scale climate patterns and the timing of spring snowmelt, although these relationships varied spatially. Fertility was weakly correlated to population density for the subpopulation on a south-facing slope, but this was not consistent across the entire study area. The census data was then used to conduct the first population viability analysis (PVA) for any member of the Ochotonidae. Several of the increasingly optimistic scenarios explored in the PVA indicated pikas in the Ruby Range are in danger of extirpation within 50 years. The observed population decline was likely due to climate-mediated variation in spring snowmelt patterns that affected subsequent adult survival through delayed onset of haying.

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My project made extensive use of data that would not exist without the efforts of many field assistants, post-docs, and graduate students. In some cases I used the data directly (e.g., pika census data) while other data were used to place my results within the greater context of alpine ecology. Thanks to Ryan Danby, Matt Mitchell, Saewan Koh, Tim Karels, Liz Gillis, Scott Wilson, Terra Birkit, Peter Caputa, Graeme Pelchat, Aaron Donahue, Alex Taylor, Ruwan Fernando, Sarah Trefry, and James Hudson for much appreciated contributions to this thesis.

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My wife, Ellen, maintained my other research site in Edmonton. Together we conducted an experiment involving the developmental biology of small humanoids and the effects of sleeplessness. This experiment was replicated twice during the course of this thesis and is expected to become a long-term project. Ellen was the principal investigator in Edmonton while I was in the Yukon and she'll never know how much I appreciated her support.

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CHAPTER 1: GENERAL INTRODUCTION

Rationale & Context

The foraging decisions made by herbivores influence their population dynamics through effects on energy gain, energy expenditure, and ultimately survival (McNamara and Houston 1997). In turn, foraging by herbivores may influence the amount of vegetation available to them in the future. Therefore, herbivores and vegetation often are coupled in a strong reciprocal relationship where the abundance of one affects the abundance of the other through time (Caughley 1976, Illius and O'Connor 1999, 2000).

Foraging decisions are constrained by a number of factors that may be classified as either internal (such as energetic or nutritional needs), or external (such as predation risk or interspecific interactions). These constraints limit the availability of forage to the herbivore and explain why most species exhibit some degree of diet selectivity (Crawley 1983, Stephens and Krebs 1986). Most herbivores, therefore, must balance trade-offs associated with these constraints, such as obtaining enough food while minimizing predation risk (Lima and Dill 1990), or decisions about selecting species with differing degrees of nutritional value (Belovsky 1978, Stephens and Krebs 1986).

Plant – herbivore interactions are particularly important for herbivores living in seasonal environments because food abundance and quality vary dramatically between growing and winter seasons. Herbivores must adapt their foraging behaviour to contend with these changes and survive until the following growing season (Owen-Smith 2002a,b,c).

Some species, such as the collared pika (*Ochotona collaris*, Figure 1-1), survive winter by caching large amounts of vegetation during the summer growing season for use during winter (Vander Wall 1990). Pikas appear to at least partially depend on their haypiles for survival during winter (Millar and Zwickel 1972, Conner 1983, Dearing 1997), and are known to have reciprocal effects on vegetation species diversity, above-ground biomass, leaf demography, and growth form (Huntly 1987, McIntire and Hik 2002, 2005). Therefore, a complete understanding of pika population dynamics requires information regarding both direct and indirect trophic interactions.

Pika Ecology & Evolution

Pikas are small (~160g) lagomorphs that diverged from other members of the Lagomorpha (i.e., hares and rabbits) in Asia 25-35 million years ago during the Oligocene epoch (Dene et al. 1982, Grillitsch et al. 1992). Currently there are 30 species of pika (Hoffmann and Smith 2005).

Pika species may be grouped into two main groups: those that occupy steppe & forest habitats, and those that occupy alpine talus habitats (Smith et al. 1990). The two groups are morphologically similar, but differ in their life histories (Smith 1988, Smith et al. 1990). Relative to steppe-dwelling pikas, talus-dwelling pikas have smaller litter sizes (1-6 young per litter for talus dwelling species versus 1-13 for steppe species), fewer litters per year (1-3 versus 3-5), and are slower to become reproductively mature (yearlings versus young of the year) (Smith 1988, Smith et al. 1990). Talus-dwelling pikas live as mated pairs in Asia but live asocially in North America (Smith et al. 1990, Smith and Weston 1990).

The collared pika is one of two pika species within North America, the other being the American pika (*O. princeps*). The collared pika's range includes the mountainous areas of Yukon, northern British Columbia, western Northwest Territories, and Alaska (Broadbooks 1965, MacDonald and Jones 1987) while the American pika's range includes the mountain areas from mid-British Columbia south to Nevada (Smith et al. 1990) (Figure 1-2).

Both North American species appear to have similar life histories (Smith 1988, Franken 2002). Populations of both species are structured as metapopulations in which naturally fragmented habitat patches (talus) are separated by an inhospitable matrix of meadow (e.g., Figure 1-3). Long-term patch occupancy data for *O. princeps* at Bodie, California showed that patch occupancy patterns were consistent with a history of patch colonization-extinction events (Moilanen et al. 1998). Patch colonization at the Bodie site was correlated to inter-patch distance (i.e., connectivity) while extinction was associated with patch area (Smith and Gilpin 1997). Similarly, Franken and Hik (2004) analyzed patch occupancy data for *O. collaris* in southwest Yukon and reported that patch colonization was best explained by aspect and habitat quality while talus extinction was related to connectivity and habitat quality. Clinchy et al. (2002) reanalyzed the Bodie dataset and concluded that the observed patterns of occupancy also were consistent with spatially correlated patterns of predation. That analysis, however, was critiqued by Lambin et al. (2004) for implausible assumptions regarding predation patterns, pika dispersal behaviour, and gene flow.

Two diets are collected during the summer growing season including i) a maintenance diet that is consumed immediately, and ii) vegetation cached within the talus (in 'haypiles'; Figure 1-4) for consumption during the winter (Conner 1983, Huntly et al. 1986). Gazing pikas appear to select different species while haying than while grazing. For example, short graminoids were more commonly selected while grazing relative to haying, while forbs and woody shrubs were more frequently selected while haying than while grazing (Huntly et al. 1986). Plant defensive compounds (e.g., phenols) have also been reported as a selection factor while haying, but not while grazing (Dearing 1996). Pikas also remain closer to talus while grazing than while haying (Huntly et al. 1986).

Pikas are central place foragers and create a strong grazing gradient of decreasing intensity from the talus edge into the meadow to a maximum distance of 6-8m (Huntly et al. 1986, Huntly 1987, McIntire and Hik 2005). Restriction of foraging activity to 6-8m from talus appears to be in response to predation risk rather than costs associated with handling time (Holmes 1991).

Pikas are sensitive indicators of climate influences because of their intolerance of warm daytime temperatures (Smith 1974) and inability to withstand freeze-thaw events during winter (Smith et al. 2004). Several studies have suggested that pikas are in danger of extinction in many regions because of global climate change (McDonald and Brown 1992, Beever et al. 2003, Grayson

2005, Parmesan 2006). Extinction patterns of montane mammals from isolated peaks in western USA were analyzed using a nested-subsets approach and indicated that *O. princeps* was particularly at risk of extinction due to climate change (McDonald and Brown 1992).

Research Objectives and Thesis Organization

Because pikas are closely tied to their vegetation resources, it follows that an understanding of their population dynamics must consider the influences of their foraging choices. This dissertation addresses several questions related to pika foraging behaviour and population dynamics:

- How does predation risk affect forage species selection?
- What role does forage quality play in selection among forage species and selection of individuals within a species?
- Do pikas hoard sufficient vegetation to serve as the sole source of food during winter?
- What effect does the annual timing of vegetation hoarding have on over-winter survival?
- What has been the contribution of survival and reproduction to observed variation in population growth rate?
- How do population density and climate patterns affect survival and reproduction?
- Given the observed variation in population abundance, what is the viability of the pika population over the next 50 years?

Study Area

All research presented in this dissertation was conducted in a 4-km^2 alpine valley within the Ruby Range, east of Kluane Lake, Yukon, Canada (61°13' N, 138°16' W; 1600-2200 a.s.l) (Figure 1-5). The site was representative of the Ruby Range, but pikas living west of the St. Elias Mountains experience different climate, vegetation, and topography (Theberge 1980).

Collared pikas have been studied at this site since 1995, Arctic ground squirrels (*Spermophilus parryii)* from 1998 to 2002 (Gillis 2003), and hoary marmots (*Marmota caligata*) from 1999 to 2004. These three species are the dominant mammalian herbivores at this site and provide context for my research on foraging behaviour and population dynamics. The effects of observers on pika behaviour are unknown. However pikas did not alarm call or attempt to hide while in close proximity (<10m) to observers. Pikas grazed and hayed in meadows and regularly traveled near observers (i.e., relatively risky behaviours) suggesting pikas did not perceive observers as threats.

Vegetation has been studied with respect to 1) simulated climate change (Tait 2002), 2) response to herbivory by pikas (McIntire and Hik 2002, 2005), and 3) competition and facilitation (Mitchell 2006). Therefore, plant community dynamics are well understood in this alpine system.

The southwest Yukon has experienced rapid warming since instrumental record keeping began (Zhang et al. 2000) and this trend is expected to continue (Laprise et al. 2003, ACIA 2005). Because pikas are sensitive indicators of climate change (Smith 1974, McDonald and Brown 1992, Beever 1999, Smith et al. 2004, Grayson 2005), our study site was particularly well suited for studies of pika foraging behaviour and population dynamics in the context of a changing and increasingly variable climate.

Chapter Descriptions

The specific rationale, underlying theoretical basis, and specific objectives are provided in the introduction to each chapter. I briefly describe each chapter below and direct the reader to individual chapters for additional details. The final chapter of this dissertation is a synthesis and suggests new research directions.

In **Chapter 2**, I experimentally addressed how variation in predation risk affects haying behaviour using a series of cafeteria trials at varying levels of predation risk. Predators may affect prey population dynamics directly through mortality, or indirectly through changes in prey behaviour or physiology in response to predation risk (Lima and Dill 1990, Sinclair and Arcese 1995). These sub-lethal effects often are independent of actual predation (Lima 1998) and may have large effects on prey populations (Schmitz et al. 1997). Sub-lethal predation effects may have important consequences for pika population dynamics because i) pikas are sensitive to predation risk (Holmes 1991), ii) haypile accumulation is a core part of pika summer behaviour (Smith and Ivins 1986, Smith et al. 1990, Dearing 1997) and iii) haypile mass is thought to have important over-winter survival consequences.

Multiple nutritional constraints often are responsible for the preferences for certain forage species (Belovsky 1978), and this leads to a diet composition that differs from the availability of species within its environment. In **Chapter 3**, I experimentally examined how forage quality affects the selection of vegetation for storage in haypiles. Several factors have been hypothesized to explain how pikas select forage species, including nitrogen (Millar 1971, Holmes 1991) and water content (Smith 1974). I used a series of cafeteria-style trials, similar to Chapter 2, in which I manipulated crude protein and water content of two common forage species in a factorial design to determine how pikas made inter- and intra-specific choices regarding vegetation selection for use during winter.

The importance of haypiles for the over-winter survival of pikas is unresolved (Millar and Zwickel 1972, Conner 1983, Dearing 1997). I addressed this issue (**Chapter 4**) by estimating haypile mass in two ways: 1) intensive video surveillance of haypiles, and 2) excavating known haypiles at the end of summer. Haypile mass was then converted into the number of days of available food based on known rates of vegetation consumption in winter.

Chapter 5 addresses whether the annual timing of initiation of vegetation caching ('haying') by pikas has an effect on over-winter survival. Because haypile location is relatively invariant across years it was possible to closely monitor these locations for evidence of haying activity. The effect of when annual haypile accumulation began on over-winter survival was then evaluated using classification trees (Breiman et al. 1984).

The influence of population density and large-scale climate patterns on population demographics and dynamics is addressed in **Chapter 6**. Annual projection matrices based on a post-breeding census design (Caswell 2001) were constructed using long-term trapping data. A life-table response experiment (LTRE) was then conducted on the matrices for the entire population, and separately for each of three sub-populations defined by topography and animal movement data. The second component of this chapter was to determine the mechanistic basis underlying variation in vital rates, and therefore, population growth. To do so, we evaluated the effects of population density and the Pacific Decadal Oscillation, the dominant climatic pattern in the region, on the vital rates that contributed most to variation in population growth.

Chapter 7 used data from Chapter 6 to conduct a demographically-based population viability analysis (PVA) of the pika population at our site following the methods of Morris and Doak (2002). This chapter considered several scenarios from most realistic (using all available data) to most optimistic (using highest quality sites and years of highest survival). This chapter constituted the first PVA for any species within the Ochotonidae, and is particularly timely given the reports of declines in several other pika species (e.g., Smith et al. 2004, Grayson 2005, Li and Smith 2005).

Overall, this dissertation uses a combination of manipulative (Chapters 2 and 3) and mensurative (Chapters 4 and 5) experiments, combined with matrix population models (Chapters 6 and 7) to understand how pikas select vegetation for use during winter, the impact of haying behaviour on over-winter survival, and the drivers and consequences of observed population dynamics via climate influences on spring snowmelt patterns and forage availability. In doing so, we are able to increase our understanding of climate-plant-herbivore systems, and the influence of foraging decisions on herbivore population dynamics in alpine environments.

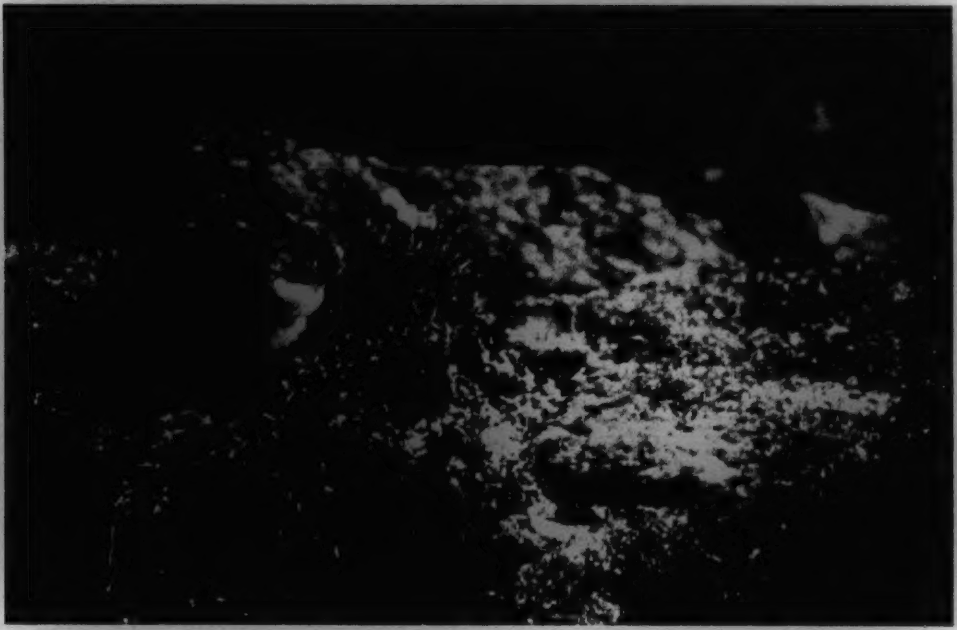

Figure 1-1: Collared pika (*Ochotona collaris*) with a metal eartag and red colored wire to facilitate identification.

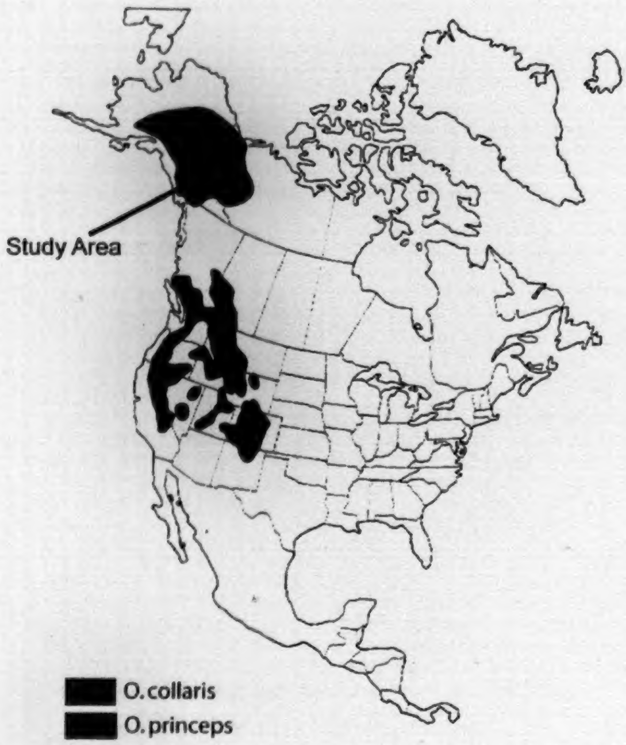
Study Area
O. collaris
O. princeps

Figure 1-2: Species range of collared (*O. collaris*) and American (*O. princeps*) pikas. Image modified from Smith et al. (1990).

Figure 1-3: West-facing view of the Ruby Range study area showing talus patches interspersed with alpine meadow.

Figure 1-4: Pika haypile under talus in late summer.

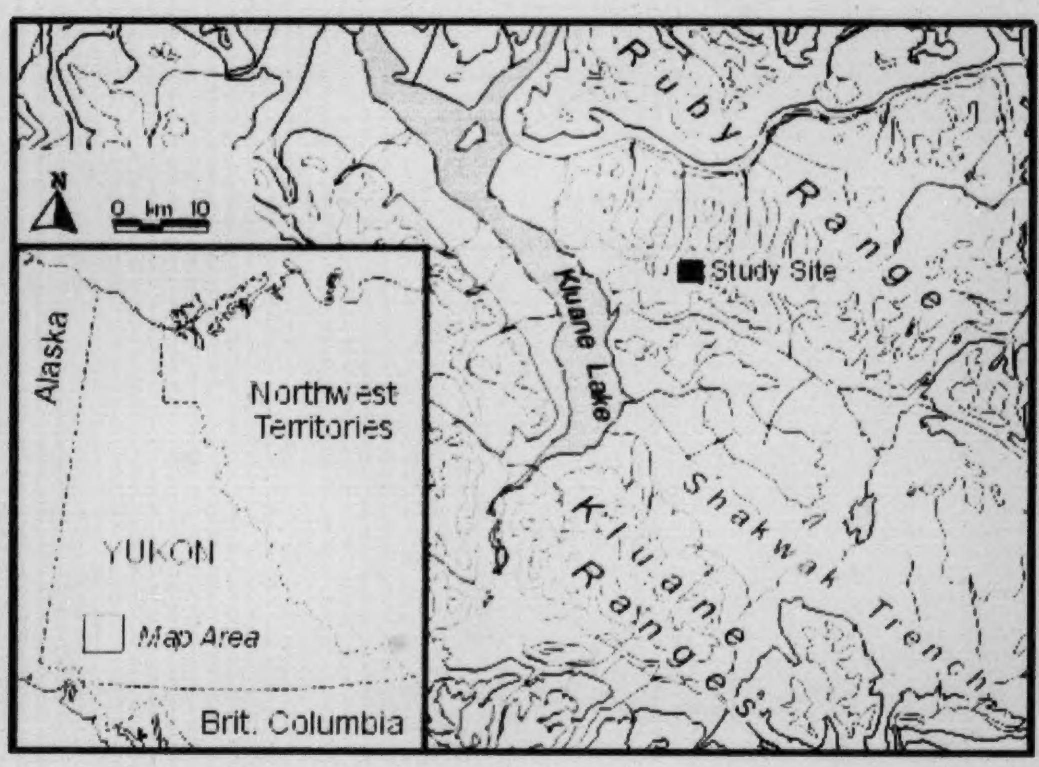
Ruby Range
0 km 10
N
Study Site
Kluane Lake
Alaska
Northwest Territories
YUKON
Map Area
Brit. Columbia
Shakwak Trench
Kluane Ranges

Figure 1-5: Location of study site within the Ruby Range, east of Kluane Lake, southwest Yukon.

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CHAPTER 2: FORAGE SELECTIVITY BY COLLARED PIKAS, *OCHOTONA COLLARIS*, UNDER VARYING DEGREES OF PREDATION RISK *

Introduction

Predators may affect prey population dynamics directly through mortality, or indirectly as a result of changes in prey behaviour or physiology in response to predation risk (Lima and Dill 1990, Hik 1995, Sinclair and Arcese 1995, Lima 1998). These sub-lethal effects often are independent of actual predation (Lima 1998) and may have large effects on prey populations (Schmitz et al. 1997) and community structure (Hughes et al. 1994). Sub-lethal effects derive from changes in social interactions, mating opportunities, microhabitat use, and foraging behaviours of prey to reduce their risk of predation (Caraco 1980, Bowers and Dooley 1993, Hik 1995). These changes often result in lower energy intake, poorer body condition (Hik 1995, Sinclair and Arcese 1995), and reduction in long-term reproductive output (Dill 1987, Boonstra et al. 1998, Lima 1998).

Prey species evolve to avoid being killed, and their predators evolve to improve their success at catching prey. However, at more proximate time scales it is useful to ask questions about how prey species may alter their behaviour in response to varying levels of predation risk since this has "important implications for behavioural, evolutionary and community ecology" (Sih 1984, p. 149). The sub-lethal effects of predation risk on foraging behaviour result in a trade-off between obtaining food and safety (Lima and Dill 1990, Brown 1992), but changes in selection of individual forage species has received relatively less attention. An examination of forage selectivity under varying levels of predation risk will provide insights about how herbivores decide which plant species to consume (e.g., Basey and Jenkins 1995), and this has implications for nutrient intake and thus long-term reproductive output and survival.

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We tested the effects of predation risk on forage selectivity and consumption using the collared pika (*Ochotona collaris*) as a model species. Pikas are small (~160g) central-place foragers inhabiting talus slopes in alpine and subalpine regions of Yukon, Alaska, northern British Columbia, and western Northwest Territories (Broadbooks 1965, Smith et al. 1990). Although they are thought to be similar to the American pika (*O. princeps*), few studies have been published regarding their ecology and behaviour (Broadbooks 1965, MacDonald and Jones 1987). During the growing season (June - August), pikas graze plants near talus patches and collect large amounts of vegetation that they store in haypiles within the rock matrix of talus slopes for use during winter (Millar and Zwickel 1972, Dearing 1997a). Pikas do not cooperate in building haypiles and territories are aggressively defended against conspecifics (Conner 1983).

Pikas are behaviourally restricted to talus slopes and rarely venture >10m into meadows (Huntly et al. 1986, Roach et al. 2001, McIntire and Hik 2002). Restriction to talus is a function of several factors including predation risk (Huntly et al. 1986) and thermoregulation (Smith 1974). The predation risk hypothesis was supported by Holmes (1991) who demonstrated that collared pikas increased the distance they foraged from talus when talus was artificially extended into the meadow. Talus contains many cavities and crevasses that provide pikas with important escape opportunities from predators (Ivins and Smith 1983).

Differential selection of food items may result from a trade-off between the value of food items and the probability of being attacked by a predator (O' Dowd and Hay 1980, Lima et al. 1985, Leaver and Daly 2003). Hay and Fuller (1981) showed that vulnerability to predation was a major influence in determining the types of food selected by rodents within microhabitats of differing predation risk. Further, predation is also believed to influence when foragers stop feeding at a patch, with the amount consumed inversely related to predation risk (Valone and Brown 1989, Jacob and Brown 2000). For example, Longland (1991) reported that black-tailed jackrabbits (*Lepus californicus*) forage intake declined as predation risk increased with distance from protective shrubs.

Since haying pikas are sensitive to predation risk, with risk increasing with distance from talus, we predicted: 1) selectivity for individual forage species would change relative to other species with increased distance from talus, 2) the amount removed during haying would be inversely related to distance from talus, 3) addition of talus cover would decrease the effects of predation risk in meadows, and 4) forage selectivity and removal within talus (where predation risk is homogenous) will not vary with distance from the haypile, assuming that the frequent movements of pikas familiarize them with escape passages throughout their home range.

Methods

STUDY AREA

The study was conducted in a 4-km^2 alpine meadow interspersed with talus slopes in the Ruby Range, east of Kluane Lake, Yukon, Canada (61°13'N, 138°16'W) between 28 July and 22 August 2000, and 30 July and 16 August, 2002. Collared pikas, hoary marmots (*Marmota caligata*) and Arctic ground squirrels (*Spermophilus parryii*) were the dominant herbivores in the valley and have been studied there since 1995 (Hik et al. 2001). Pika populations tripled during the course of this study from 1.5 pikas/ha in 2000 to 4.7 pikas/ha in 2002 (Franken 2002; Chapter 6). Marmot populations have remained relatively constant (Karels et al., unpublished data). Potential predators of pikas include raptors, red foxes (*Vulpes vulpes*), and weasels (predominately short-tailed weasels, *Mustela erminea*) (Hik et al. 2001).

EXPERIMENTAL SYSTEM

Collared pikas offer a useful experimental system in which to test foraging theory. Territories are usually <50m in diameter (Franken 2002) and pikas quickly habituate to observers allowing for close observation (Chapter 1). They rarely venture further than 10m into meadows, creating a strong gradient of grazing pressure where most foraging activity occurs within 3m of talus (Huntly 1987, McIntire and Hik 2005). Since pikas appear to be sensitive to predation risk (Holmes 1991), are easily observed, and are insatiable hoarders of vegetation (Smith and Ivins 1986, Mckechnie et al. 1994), they are a suitable species to study the effects of predation risk on the selection of forage species. Vegetation experimentally placed within their territories during the latter half of the growing season when haying activity is at its peak is quickly discovered and transported to haypiles.

Previous research on *O. princeps* in Colorado showed that forage selection while haying is positively associated with the presence of plant secondary compounds (i.e., phenols) which may reduce over-winter decomposition of stored vegetation in haypiles (Dearing 1997b). In contrast, at our high-latitude study site, secondary compounds are generally absent or weak (Jung et al. 1979, Hik et al. 2003), greatly reducing this as a potentially confounding factor from our experiments.

CAFETERIA TRIALS

Forage preferences of haying pikas were determined using a cafeteria-style preference experiment. The cafeteria was constructed of six adjacent polyvinylchloride (PVC) tubes (diameter = 10cm, length = 15cm) that were capped at one end and laid on their sides. For each trial, 15g (± 0.1g) fresh-weight of each forage species (*Artemisia norvegica*, *Polygonum bistorta*, *Carex spp.*, *Salix reticulata*, *Dryas octopetala*, and *Cassiope tetragona*; Appendix A) were randomly allocated to a separate tube. The six forage species were selected for this experiment based on their abundance and occurrence in haypiles (Appendix B) and surrounding meadows, and their relative rankings in previous studies of forage selectivity by collared pikas (D.S. Hik, unpublished data).

Because pikas are individually territorial, placement of cafeterias within territories allowed us to target individual pikas. All trials were conducted between 1000 and 2300 hrs and each trial was run for a maximum of 4h. Only one treatment was presented to a given pika at any given time. Once the targeted pika began to remove vegetation from the cafeteria (i.e., haying), cumulative selection (% removed) for each species was recorded at 0.5h intervals for the duration of the trial. We were able to minimize the potentially confounding effect of water loss from the vegetation as the trial progressed by estimating the percentage removed, rather than relying on changes in absolute mass.

Cafeterias were observed periodically to ensure only the targeted pika was removing vegetation. Trials were stopped and excluded from analysis if other pikas began removing vegetation from the cafeteria (2 of 52 trials). Trials for a given pika were separated by at least 6 hrs, and usually only one trial per day was conducted. While individual trials were not continually observed, at least one trial was under observation at all times. These observations, and other independent observations from other experiments indicated that >99% of all removed vegetation was due to haying activity and not to grazing (direct consumption) by pikas. Therefore, our data reflected selection by haying pikas only and are not confounded by the possibility of grazing, with possibly different selection criteria.

Trials were conducted across five treatments which reflected perceived predation risk and costs associated with travel: 1) <4m from a haypile (HP) in talus, 2) 16m from HP in talus (to reflect the radius of an average territory (Franken 2002)), 3) 2m into a meadow, 4) 4m into a meadow, and 5) 4m into a meadow with artificially added talus cover. Treatment 2 was conducted to serve as a control for the energetic and thermoregulatory costs associated with haying. Distances from talus were selected to reflect incremental increases in predation risk within the zone used most frequently by foraging pikas. Treatments 4) and 5) were conducted in the same location, the only difference being the presence or absence of talus cover. In 2002, we also conducted trials at 8m into the meadow with no added talus cover. However, sample size was low and we did not have matching trials from 2000, so excluded it from statistical analysis.

Selection indices were calculated using Rodgers' Index (Equation 1, Rodgers and Lewis 1985, Krebs 1999):

$$R_i = \frac{A_i}{\max(A_i)}$$

where R_i is Rodgers' Index of preference for species *i*, A_i is the area under the cumulative proportion eaten curve for species *i*, and $\max(A_i)$ is the largest value of A_i for that cafeteria trial. This index is the most appropriate method for analysis of cafeteria-style experiments where available forage is depleted during the trial. Misleading selection indices may be calculated if only the mass or amount remaining at the end of the trial is used as an index of preference because some species may not have been consumed until other, more preferred, species were eaten first (Krebs 1999). Rodgers' Index avoids this problem by calculating selection based on the cumulative proportion consumed for each species during the course of the trial. The amount consumed was evaluated by using the proportion of each species removed at the end of each trial.

Rodgers' selection indices and proportions were arcsine transformed to approximate a normal distribution (Krebs 1999, Zar 1999). Each dataset was analysed separately with a 3-way analysis of variance (ANOVA) with treatment, year, and forage species as fixed factors. Post-hoc pair-wise comparisons were made using Tukey's test (Zar 1999).

A significant Treatment × Species interaction term in the ANOVA using Rodgers' Indices would indicate that pikas change their relative preferences based on treatment. Note that a significant Treatment term alone is not sufficient to conclude changing species preferences because individual species are not considered. Instead, a significant Treatment term could reflect changing consumption since Rodgers' Index relies on the amount of forage removed in addition to relative order of selection. To confirm if total consumption varies with predation risk (i.e., Prediction 2), a significant Treatment term must be present in the ANOVA results based on proportion data.

Results

Data for each sex initially were analyzed separately. Similar significant (all $P < 0.05$) and non-significant ($P > 0.71$) results were obtained for each sex so males and females were pooled for further analysis. The patterns of foraging behaviour were consistent between 2000 and 2002 (Figures 2-1 and 2-2), even though different individuals were used in each year. We presented cafeterias to six pikas in 2000 and seven pikas in 2002 although not every treatment was presented to each individual (Table 2-1).

Contrary to our first prediction there was no significant interaction between species and treatment ($F_{20,288} = 0.53$, $P = 0.954$, Table 2-2), indicating that pikas did not alter their selectively for individual forage species as predation risk increased (Figure 2-1). A significant Treatment term ($F_{4,228} = 4.89$, $P = 0.001$, Table 2-2) suggested that selection differed among treatments; this was supported by a significant Treatment term in the analysis of proportion data ($F_{4,246} = 6.89$, $P < 0.001$, Table 2-3).

The total amount of vegetation removed by pikas decreased with distance from talus (Figure 2-2), consistent with our second prediction. Pikas removed the least amount of vegetation from the treatment furthest from talus (Treatment 4), but the addition of rock cover (Treatment 5) ameliorated this effect (Tukey post-hoc test, $P > 0.05$, Figure 2-2), consistent with our third prediction. Both selection and proportion of vegetation removed by pikas differed by year (Tables 2-2 and 2-3, respectively). The significant interaction between year and species ($F_{5,228} = 3.40$, $P = 0.006$, Table 2-2) on selection indicated that selection of individual species differed between 2000 and 2002. This interaction seemed to be a result of pikas selecting more *D. octopetala* and *S. reticulata* in 2002 than in 2000 (Figure 2-2). Increased selection, as measured by Rodgers' Index, is either a function of the total amount of vegetation removed from the cafeteria during the trial, the rate at which it was removed, or both (Krebs 1999). Analysis of the total amount of vegetation removed provides only weak support ($F_{5,246} = 1.95$, $P = 0.087$, Table 2-3) that increased selection was due to more *D. octopetala* and *S. reticulata* being removed in 2002 than 2000. Consequently, it is likely that rates of removal were higher in 2002. Rank selection order of forage species mirrored nitrogen content ranking in 2000 (Table 2-4). In 2002 there were no obvious trends, when rank selection was compared to the 2000 nutritional data.

Discussion

Contrary to our first prediction, pikas did not become more selective for individual forage species as predation risk increased, although they did take less forage overall. We predicted pikas would change their preferences for individual forage species as predation risk increased (e.g., O' Dowd and Hay 1980, Basey and Jenkins 1995), such that pikas would select all species when predation risk was minimal (i.e., within talus patches), and become more selective as predation risk increased further into the meadow. Since the species we presented had a range of digestibility (Andruchow 2000) and nitrogen content (Table 2-4), we expected that pikas would choose only those of greatest nutritional value (e.g., *A. norvegica*) and ignore those of lesser value (e.g., *D. octopetala* and *C. tetragona*) when predation risk was highest. Our results (i.e., no Treatment × Species interaction), however, do not support this prediction and suggest that pikas did not change forage preferences as predation risk increased. Similar results have been obtained for snowshoe hares (*Lepus americanus*) during the low phase of their cycle (Hodges and Sinclair 2003). In that study, hares selected forage based on protein and fibre content regardless of predation risk.

At greatest predation risk (Treatment 4) pikas took less forage than any other treatment. Consumption of less forage at greater levels of predation risk has been documented previously in small mammals (Valone and Brown 1989, Kieffer 1991, Kotler et al. 1992). Keiffer (1991) attributed this to increased hesitance in approaching distant (i.e., risky) food and increased vigilance at the expense of foraging time. Pikas, however, are less vigilant while haying and therefore vigilance is not a plausible explanation for reduced haying activity in our experiment.

Pikas were observed haying at cafeterias up to 8m into the meadow when trained to use the cafeteria. The cost of searching for and harvesting food from the cafeteria was minimal and the only costs were travel time and predation risk. Since the costs of travel associated with haying are likely minimal it is possible that pikas were able to obtain enough forage to offset the cost of traveling further into the meadow without protective talus cover. Indeed, the extent to which animals may be induced to expand their movement patterns may be used to measure the influence of predation risk (Anderson 1986). Although pikas could be induced to travel further from talus cover, the amount of forage removed at this distance was less than from feeders closer to cover, once again reflecting the influence of predation risk on giving up densities.

The addition of protective rock cover at 4m into the meadow (Treatment 4) ameliorated the effects of predation risk (Treatment 5) and the consumption of forage approximated that of treatments with less predation risk. This supports Holmes' (1991) assertion that predation risk alone limits pikas to the narrow band of vegetation surrounding talus patches.

The reasons underlying the difference in selection between 2000 and 2002 are unknown but there are at least two possible explanations. First, pika densities tripled between 2000 and 2002 (Franken 2002). Higher densities may have caused greater competition for forage and resulted in the increased use of *S. reticulata* and *D. octopetala*, as expected from optimal diet theory (Pulliam 1974). Alternatively, increased selection of these species in 2002 may be a function of improved nutritional quality since that year had a longer growing season than 2000 (D. Hik, unpublished data).

For within-talus treatments (Treatments 1 and 2), neither relative selection nor the proportion of forage taken varied with distance from the haypile. Since predation risk is likely equivalent within talus (where there are numerous familiar cavities among the rocks for hiding and escape), any difference in forage selection or consumption must be associated with other costs, such as travel time. We observed no difference between the close (Treatment 1) and far (Treatment 2) treatments, suggesting that travel costs for haying pikas are minimal. Since pika territories are approximately 20m in radius (Franken 2002), a lack of an effect at 16m implies that travel costs are minimal within an individual's home range.

Pikas at our study site often are associated with *C. tetragona* communities (Franken 2002). However, *C. tetragona* is not extensively used by pikas for forage, probably because of its low nitrogen, digestibility, and water content (Andruchow 2000). The reasons for the association are unclear, but Franken (2002) hypothesized that pikas were unable to compete against hoary marmots at more productive sites and were thus forced to establish territories in the less-productive *C. tetragona* patches. Focal watches of hoary marmots indicated that >80% of their foraging efforts are concentrated to within 20m of talus patches, although they also forage 50-100m away from talus (Barash 1989, Karels et al. 2004). The area with highest marmot foraging activity completely overlaps foraging areas also used by pikas, and thus may exclude pikas from preferred foraging areas through either interference or exploitative competition.

In conclusion, pikas did not alter their selection of forage species based on predation risk although the total amount they removed declined at the highest level of risk. Addition of protective rock cover resulted in pikas removing more vegetation from riskier patches and supports the hypothesis that pikas are limited to talus patches by predation risk (Holmes 1991, Karels et al. 2004). The differences in selection between 2000 and 2002 raise interesting questions regarding inter-year variability in forage selection. Possible explanations for this result include inter-year variation in predation risk, forage quality, competition with hoary marmots, or body condition (Saarikko 1992).

Table 2-1: Sample size of pikas stratified by treatment and year. In each year the same individuals were used for more than one treatment. Distances for talus treatments refer to distance from the haypile, while distances reported for meadow treatments are distances to the margin of the nearest talus patch. All talus treatments, by definition, had talus cover.

Treatment	Description	# pikas 2000	# pikas 2002
1	In talus, 4m from haypile	5	7
2	In talus, 16m from haypile	5	6
3	In meadow, 2m from talus edge	4	6
4	In meadow, 4m from talus edge, with no added cover	6	5
5	In meadow, 4m from talus edge, with added cover	5	5

Table 2-2: Analysis of variance to determine effects of predation risk on forage selectivity as measured by Rodgers' Index.

Source	SS	Df	MS	F	P
Year (Y)	4.32	1	4.32	28.67	<0.000
Species (S)	53.05	5	10.61	70.35	<0.000
Treatment (T)	2.95	4	0.74	4.89	0.001
Y × S	2.57	5	0.51	3.40	0.006
Y × T	0.24	4	0.06	0.40	0.806
S × T	1.59	20	0.08	0.53	0.954
Y × S × T	2.04	20	0.10	0.68	0.849
Residuals	34.39	228	0.15		

Table 2-3: Analysis of variance to determine effects of predation risk on proportion of vegetation removed from cafeteria-style feeders.

Source	SS	df	MS	F	P
Year (Y)	2.94	1	2.94	17.86	<0.000
Species (S)	59.84	5	11.97	72.68	<0.000
Treatment (T)	4.54	4	1.13	6.89	<0.000
Y × S	1.61	5	0.32	1.95	0.087
Y × T	0.13	4	0.03	0.20	0.939
S × T	2.47	20	0.12	0.75	0.773
Y × S × T	1.66	20	0.08	0.50	0.964
Residuals	40.51	246	0.17		

Table 2-4: Rank order of six common forage species in relation to nitrogen content, digestibility, and water content based on data from Andruchow (2000). Actual values are given in parentheses. Data for *D. octopetala* were stratified by leaves and flowers, respectively.

Forage Species	Nitrogen	Digestibility	Water
A. norvegica	1 (2.8)	1 (60.2)	1 (80.2)
P. bistorta	2 (2.2)	4 (45.7)	2 (77.8)
Carex spp.	3 (2.0)	3 (46.6)	5 (61.8)
S. reticulata	4 (1.9)	2 (52.1)	3 (65.6)
D. octopetala	5/5 (1.8/1.8)	5/7 (42.8/29.3)	6/4 (57.3/64.0)
C. tetragona	6 (1.0)	6 (33.5)	7 (41.4)

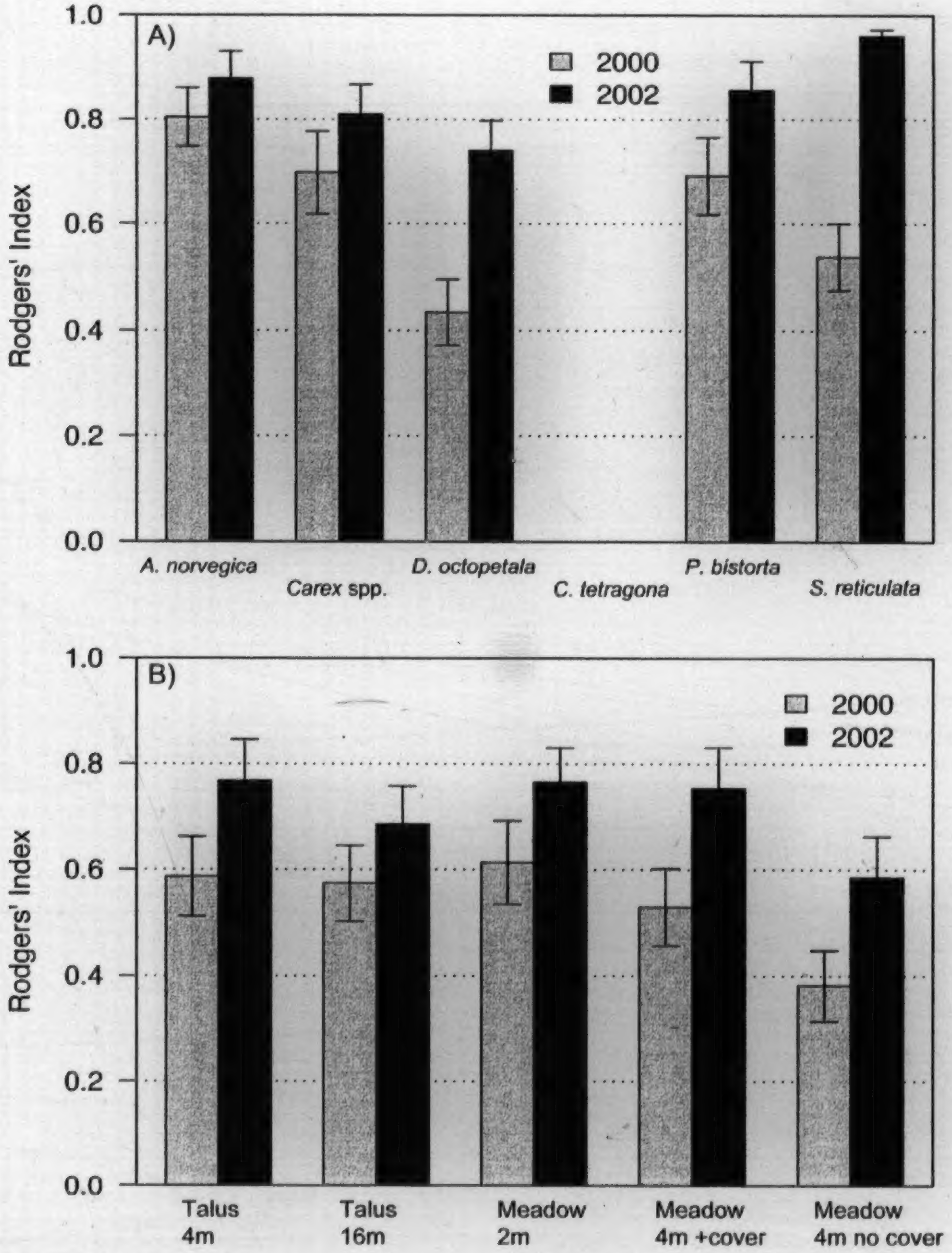

Figure 2-1: Forage selection ($\bar{x}$ ± s.e.) stratified by A) forage species and B) treatment for pikas in late summer 2000 and 2002.

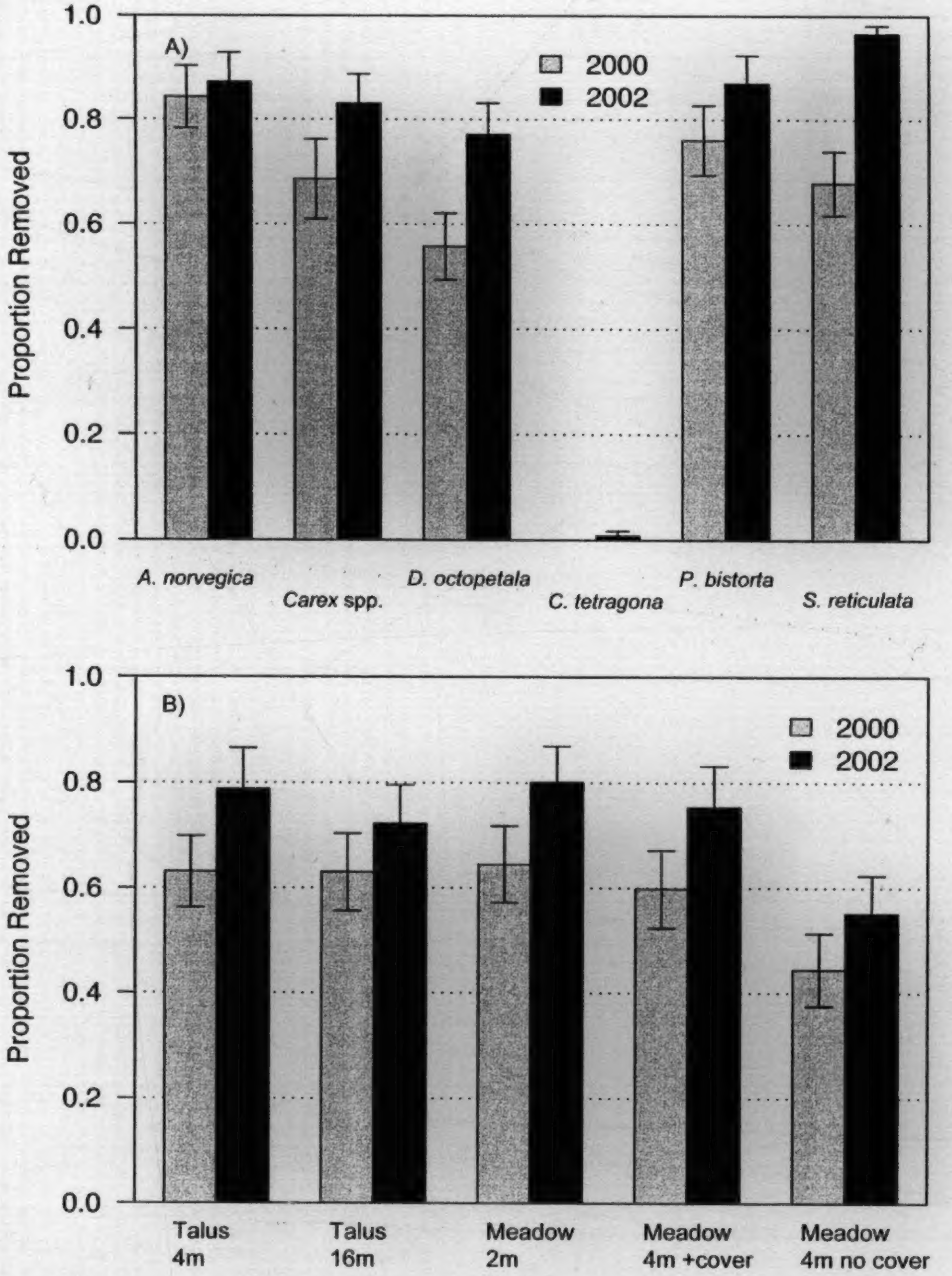

Figure 2-2: Proportion of vegetation removed from cafeterias ($\bar{x}$ ± s.e.) stratified by A) forage species and B) treatment for pikas in late summer 2000 and 2002.

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CHAPTER 3: DISCRIMINATION OF INTRA- AND INTER-SPECIFIC FORAGE QUALITY BY A GENERALIST HERBIVORE

Introduction

Herbivores face a constantly changing selection of forage in terms of quality, abundance and accessibility, and this complexity forces herbivores to make numerous decisions regarding diet selection (Stephens and Krebs 1986, McNaughton and Banyikwa 1995). This continuous assessment of multiple nutritional and physiological constraints (Belovsky 1978, Robbins 1983, Stephens and Krebs 1986, Belovsky and Schmitz 1991) may lead to a diet composition that typically differs from the average availability of forage species. An individual's nutritional environment is more complex than simply ranking available forage species, therefore it is desirable to understand the specific nutritional characteristics by which herbivores evaluate their foraging options (Robbins 1983). Herbivores also may be constrained by chemical and physical plant defences, the amount of time per day available for foraging, or other factors (Stephens and Krebs 1986).

Protein acquisition has important life history and population-level consequences because the constituent components, amino acids, are essential to support herbivore growth and reproduction (Robbins 1983, Schetter et al. 1998). The protein content of forage also reflects dry matter digestibility and therefore its energetic value (Robbins 1983). Nitrogen (or protein) content often is limiting for small mammalian herbivores (Robbins 1983, Parsons et al. 2005) and experimental addition of nitrogen to vegetation often increases the population abundance of small mammalian herbivores, although increased reproduction is often confounded by immigration (Grant et al. 1977, Boonstra et al. 2001).

Food intake is constrained by the volume of the herbivore's alimentary system where there is a finite amount of space in which to hold ingested forage. The water content of forage (e.g., the ratio of wet mass to dry mass) is commonly used as a measure of this constraint (Belovsky 1984, Belovsky and Schmitz

1991, Schmitz et al. 1992) because it reflects plant bulk. Greater water content means the digestive tract will be filled more rapidly at the expense of ingesting less dry matter, and therefore less protein or energy. Therefore, herbivores may select against forage species with relatively high water content.

Alternatively, higher water content may also reflect higher digestibility. Partially drying forage (e.g., as occurs with cached vegetation) decreases its digestibility because the relatively digestible cytoplasm is metabolized during the time the plant continues respiration. The remaining cell wall is typically high in lignin and is of lower digestibility relative to the cytoplasm (Robbins 1983). Therefore, higher water content may indicate higher digestibility and nutrient availability relative to forage species with lower water content.

Most arctic and alpine ecosystems are chronically limited by nitrogen availability (Bowman et al. 1993, Chapin et al. 1995, Nilsson et al. 2002) so the effects of nitrogen availability on inter- and intra-specific forage selection by herbivores are often pronounced. We investigated the role of nitrogen content on forage selectivity by an alpine lagomorph, the collared pika (*Ochotona collaris*). Previous research on *O. collaris* and the closely related American pika (*O. princeps*) suggests there are a number of forage selection criteria used when hoarding vegetation for consumption during winter (hereafter referred to as 'haying').

First, nitrogen content modifies foraging selection such that pikas select winter diets higher in protein than diets randomly selected from the available vegetation (Millar and Zwickel 1972, Smith 1974, Holmes 1991, Dearing 1996). Feeding experiments using a range of available species show that plants were selected according to their nitrogen ranking (Andruchow 2000, Morrison et al. 2004), and pikas could be induced to modify their foraging locations to exploit patches of vegetation experimentally enriched with nitrogen (Holmes 1991).

Second, the water content of forage also appears to play a role in pika interspecific selection although the direction of its influence is not consistent. Millar (1971) and Smith (1974) reported that haying American pikas selected a winter diet higher in water content than expected by availability, but Dearing

(1996) showed that haypiles at her site had a lower water content than what was expected by availability. We are unaware of any study that considers the role of water content on the selection of individual plants within a given species (i.e., intraspecific forage selection) by pikas.

Vegetation stored in haypiles loses water content as it dries and has minimal water content relative to fresh vegetation when it is consumed months later during winter. Therefore, it is unlikely that pikas would select against water content as a digestive constraint. Higher water content also may negatively affect the amount of vegetation a pika can carry to the haypile per trip because of its increased bulk and mass.

Alternatively, pikas may select plants with higher water content because of its positive correlation to digestibility and nutrient-rich cytoplasmic contents (Robbins 1983). Observational data on *O. princeps* provides support for this hypothesis: haying pikas showed greater selection for forbs (relatively higher water content) than graminoids (relatively lower water content) (Huntly et al. 1986). Higher water content may also indicate that the plant has not yet started to senescence, and therefore has leaf tissue of higher nutritional content (Robbins 1983).

Third, research on *O. princeps* at lower latitudes showed that forage selection while haying is strongly influenced by secondary compounds. For example, Dearing (1997a,b) found that haypile composition at her sites was dominated by *Acomastylis rossii* despite having high levels of phenols. Further, phenols were more important than nutrients of plant morphology in influencing plant selection (Dearing 1996). Phenols protect plants from herbivory by reducing plant digestibility, either by binding with cellular proteins and thereby rendering them unavailable to the herbivore, or by inactivating digestive enzymes (Robbins 1983). However, the phenols within *A. rossii* also reduced over-winter decomposition of stored vegetation in haypiles and provided an additional source of food when the phenols degraded during winter (Dearing 1996, 1997a,c). Although important for *O. princeps*, defensive compounds are unlikely to be an important factor for *O. collaris* because they generally are absent or weak at high latitudes (Jung et al. 1979). The prevalence of plant defense compounds is known to decrease with increasing latitude (Levin 1976, Moody 1978, Robbins 1983), possibly in response to relatively less herbivore pressure or lower nitrogen levels (Mattson 1980). Therefore, the secondary compounds are unlikely to be a confounding factor in our study.

We experimentally manipulated the nitrogen and water content of two plant species commonly cached by haying pikas (*Carex consimilis* and *Polygonum bistorta*) to determine their influence on forage selection. Specifically, we tested the hypotheses that pikas are able to detect intra- and inter-specific differences in nitrogen and water content of forage. We predicted: 1) pikas would preferentially select vegetation with greater nitrogen content, 2) *P. bistorta* would be preferred to *C. consimilis* (Morrison et al. 2004), and 3) pikas would preferentially select vegetation with higher water content.

Methods

STUDY AREA

The study was conducted in a 4-km^2 alpine meadow interspersed with boulderfields in a valley in the Ruby Range, east of Kluane Lake, Yukon, Canada (61°13'N, 138°16'W). All trials were conducted during peak vegetation biomass (approximately 15 July - 15 August), but before vegetation senesence was observed. Collared pikas, hoary marmots (*Marmota caligata*) and Arctic ground squirrels (*Spermophilus parryii*) were the dominant herbivores in the valley and have been studied there since 1995 (Hik et al. 2001). Potential predators of pikas included raptors, red foxes (*Vulpes vulpes*), and weasels (predominately *Mustela erminea*) (Hik et al. 2001).

COLLARED PIKAS

Collared pikas are small (~160g) central-place foragers inhabiting talus slopes in alpine and subalpine regions of Yukon, Alaska, northern British Columbia, and western Northwest Territories (Broadbooks 1965, MacDonald and

Jones 1987, Smith et al. 1990). During the alpine growing season (June - August), pikas graze plants near talus patches and collect large amounts of vegetation that is stored in haypiles within the rock matrix of talus slopes for use during winter (Millar and Zwickel 1972, Conner 1983, Dearing 1997c). Pikas do not cooperate in building haypiles, and territories are aggressively defended against conspecifics (Conner 1983, Smith and Ivins 1986).

Collared pikas are behaviourally restricted to talus slopes and rarely venture >10m into meadows (Huntly et al. 1986, McIntire and Hik 2002) due to predation risk (Huntly et al. 1986, Holmes 1991), improved thermoregulation (Smith 1974), and access to cavities and crevasses that provide important escape opportunities from predators (Ivins and Smith 1983). Territories are usually <50m in diameter (Franken 2002), and pikas quickly habituate to observers allowing for close observation. As a result there is a strong gradient of grazing pressure where most foraging activity occurs within 3m of talus (Huntly 1987, McIntire and Hik 2002, 2005). Vegetation experimentally placed within their territories during the latter half of the growing season when haying activity is at its peak is quickly discovered and transported to haypiles.

FOCAL FORAGE SPECIES & MANIPULATION

Both forage species, particularly *C. consimilis*, are commonly found in pika haypiles (S. Morrison, unpublished data). *C. consimilis* is a clonal sedge with rhizomatous growth (Brooker et al. 2001) and is a member of the circumpolar *C. bigelowii* taxonomic complex, whereas *P. bistorta* is a herbaceous perennial (Cody 2000). Both species are common to circumpolar alpine tundra ecosystems (Hultén 1968, Welsh 1974, Cody 2000, Brooker et al. 2001). *P. bistorta* has higher water content than *C. consimilis* (77.8 vs. 61.8%, respectively), but approximately equal nitrogen content (2.2 vs. 2.0%) and digestibility (45.7 vs. 46.6%) (Andruchow 2000).

Nitrogen content was manipulated by adding commercial NPK fertilizer to growing vegetation during early June in 2003, 2004, and 2005, and in mid-August in 2002, 2003, 2004, and 2005. Fertilizer (9:3:4 ratio of N:P:K) was applied at 96 g/m^2 per application (i.e., twice per summer). Vegetation samples destined for nitrogen analysis were collected from the fertilized plot and from unfertilized areas during the period of cafeteria trials. These samples were air-dried in the field and oven dried upon return to the lab.

Samples were analyzed for percent nitrogen (N) using Dumas dry combustion on a Carlo-Erba 1500 NC analyzer (Strada Rivol Tana, Milan, Italy). Because proteins have approximately 16% nitrogen, we converted percent nitrogen to percent crude protein (CP) according to: $CP = N \times 100/16$ (Robbins 1983).

Water content was manipulated by air-drying vegetation several days prior to use in a cafeteria trial. Reference samples were collected to estimate total water content and water content at the time of each cafeteria trial. Reference samples were weighed to the nearest 0.01 g when fresh, when the cafeteria trial was conducted, and again following oven drying.

CAFETERIA TRIALS

Forage preferences of haying pikas were determined using a cafeteria-style randomized block feeding experiment. The cafeteria was constructed of eight (2 species × 2 water levels × 2 nitrogen levels) adjacent polyvinylchloride (PVC) tubes (diameter = 10cm, length = 15cm) that were capped at one end and laid on their sides. For each trial, 10 ± 0.1 g fresh-weight of each forage option were randomly allocated to a separate tube. Only leaves were presented (i.e., no stems, flowers, or seedheads) and we controlled for the influence of plant size by cutting leaves to 1 x 5 cm to attempt to control for any morphological cues such as plant size (Huntly et al. 1986).

Because pikas are individually territorial, placing the feeding cafeteria within territories allowed us to target specific individuals. Each cafeteria trial therefore represents the forage selection decisions of one pika. All trials were conducted between 1000 and 2300 hrs and each trial was run for a maximum of 1h. Only one trial was conducted per pika. Once the targeted pika began to remove vegetation from the cafeteria (i.e., haying), cumulative selection (%

removed) for each tube was recorded at 1-minute intervals for the duration of the trial. We were able to minimize the potentially confounding effect of water loss from the vegetation as the trial progressed by estimating the percentage removed, rather than relying on changes in absolute mass.

Each cafeteria was under constant surveillance to ensure only the targeted pika removed vegetation. Only in rare instances did a target pika consume vegetation while at a cafeteria and >99% of all removed vegetation was due to haying activity and not to grazing. Therefore, our data reflected selection by haying pikas only and are not confounded by the possibility of grazing, with possibly different selection criteria (Huntly et al. 1986, Dearing 1996).

FORAGE SELECTION

Forage selection was calculated using Rodgers' Index (Rodgers and Lewis 1985, Krebs 1999) where R_i is Rodgers' Index of preference for species *i*, A_i is the area under the cumulative proportion eaten curve for species *i*, and $\max(A_i)$ is the largest value of A_i for that cafeteria trial (Krebs 1999). This index is the most appropriate method for analysis of cafeteria-style experiments where the available forage is depleted during the trial. Misleading conclusions may be drawn if selection is based solely on the amount of vegetation remaining at the end of the trial because some species may not have been consumed until other, more preferred, species were removed (Krebs 1999).

$$R_i = \frac{A_i}{\max\left(A_i\right)}$$

Because R_i values are proportions we used an arcsine transformation to approximate a normal distribution (Zar 1999). Data were analyzed with a 3-way analysis of variance (ANOVA) with nitrogen content (fertilized or not), water content (dried or fresh), and species (*C. consimilis* or *P. bistorta*) as fixed factors. We blocked our analysis by trial. Because only one pika removed vegetation from a given trial, this is equivalent to blocking by individual pika.

Results

EFFECTS OF NPK ADDITION ON LEAF TISSUE CRUDE PROTEIN

The addition of NPK fertilizer increased crude protein levels in fertilized leaf tissue of *C. consimilis* (fertilized: 19.9 ± 0.24%, unfertilized: 15.1 ± 0.40%; $F_{1,17} = 216.8$, $P < 0.001$) and *P. bistorta* (fertilized: 23.3 ± 0.06%, unfertilized: 17.2 ± 0.81%; $F_{1,14} = 50.8$, $P < 0.001$) (Figure 3-1). Crude protein was higher in 2005 relative to 2004 for both species (i.e., a significant year effect: *C. consimilis*: $F_{1,17} = 19.8$, $P < 0.001$, *P. bistorta*: $F_{1,14} = 29.8$, $P < 0.001$). These results indicate both species were able to absorb the NPK fertilizer and had higher crude protein levels relative to non-fertilized plants. Overall, the addition of NPK increased CP levels in *C. consimilis* by 14.8 and 11.8% in 2004 and 2005, respectively. For *P. bistorta* the CP levels increased by 12.0% and 15.9% in 2004 and 2005, respectively, with the addition of NPK.

EFFECTS OF AIR-DRYING ON LEAF TISSUE WATER CONTENT

Air-drying reduced the proportional water content of *P. bistorta* from 0.81 ± 0.01 to 0.41 ± 0.03 (Figure 3-2). Similarly, the content of *C. consimilis* was reduced from 0.64 ± 0.01 to 0.33 ± 0.02 following air-drying. *P. bistorta* lost a greater proportion of water than *C. consimilis* during air drying (ANOVA, 2-way interaction, $F_{1,149} = 4.36$, $P = 0.04$). The addition of fertilizer had no effect on water content when considered as a main effect ($F_{1,149} = 0.06$, $P = 0.81$), or included in two- or three-way interactions (all $P > 0.10$) (Figure 3-2).

CAFETERIA EXPERIMENTS

Preference data were collected for 27 pikas using cafeteria-style feeding trials (4 in 2003, 18 in 2004, and 5 in 2005) and all trials were conducted between 15 July and 15 August of each year. We did not include year as a factor in the analysis because of relatively small sample sizes in 2003 and 2005, and previous experiments that indicated that there is no effect of year on selection of graminoids or herbs (Morrison et al. 2004; Chapter 2).

No main effects or 2-way interactions among the fixed factors were significant (all $P > 0.16$; Table 3-1). However, a significant three-way Species × Nitrogen × Water interaction ($F_{1,182} = 4.01$, $P = 0.047$, Table 3-1) suggested that pikas were making conditional forage selection decisions. This interaction appeared to be driven by greater selection for fresh rather than dried *C. consimilis* when both were unfertilized (Figure 3-3). This effect of water content was not detected for either fertilized *C. consimilis* or fertilized *P. bistorta* (Figure 3-3).

Discussion

Our results indicate that pikas make subtle decisions about their selection of vegetation during haying. Nitrogen and water content are known to affect inter-specific forage selection by pikas (Millar and Zwickel 1972, Morrison et al. 2004), however this is the first study to examine their influence on intra-specific selection. Our experiments indicate that forage selection is contingent on inter- and intra-specific criteria including water and crude protein content. Pikas selected unfertilized fresh *C. consimilis* over unfertilized dried *C. consimilis*, but this relationship disappeared when the crude protein content of *C. consimilis* was increased. No such relationship existed for *P. bistorta*. Pikas tended to prefer fertilized over unfertilized *P. bistorta*, regardless of water content, however this difference was not statistically significant. Holmes (1991) added ammonia nitrate to alpine vegetation causing the crude protein content of a pooled sample of multiple species to increase by 11%. This was sufficient to alter the foraging behaviour of pikas. The addition of fertilizer at our site increased the crude protein content of both *C. consimilis* and *P. bistorta* by a minimum of 11.8% and therefore should have been detected by pikas. Baker et al. (1987) suggested that detection of protein variation may be a learned response, however our study was of the same duration as Holmes (1991) who detected a strong effect of increased crude protein levels.

Haypile vegetation is air-dried prior to its consumption during winter, several months after its collection. Because water content is reduced after drying in the haypile it is unlikely that wet:dry mass as a digestive constraint was an important selection factor. Optimal foraging theory predicts that central place foragers, like pikas, should maximize the amount of energy or vegetation mass carried per trip (Stephens and Krebs 1986). Plants with greater water content (i.e., greater wet/dry mass) are more costly to harvest in terms of load size because fewer leaves can be carried per trip. Therefore, pikas may select leaves with reduced water content (less bulk) as observed by Dearing (1996) who showed that haypiles at her site had a lower water content than what was expected by availability. Our results, however, corresponded more favourably with Smith (1974) and Millar (1971) who reported that haying pikas selected plants with higher water content than a random selection of available vegetation. The water and protein content of vegetation decreases at the end of the growing season (Millar 1974). As the winter dormant season approaches alpine plants reallocate nutrients from aboveground tissues to roots and rhizomes (Vitousek 1982). If pikas were using water content as a cue for some aspect of plant quality they should chose plants with greater water content as this would indicate plants that were in earlier stages of senescence than plants with lower water levels.

One study of the closely related American pika showed forage selection was driven by the presence of phenolic secondary compounds rather than by nutrients (Dearing 1996, 1997a). The secondary compounds prevent decomposition of haypile vegetation during winter and their gradual degradation during the winter allows pikas to eventually use these plants as a winter food source. Collared pikas at our site, however, do not appear to preferentially select plant species with high levels of secondary compounds, (e.g., *Cassiope tetragona*, Morrison et al. 2004). Nevertheless, we controlled for this possibility by including forage species with low levels of defense compounds (Jung et al. 1979) and the lack of a significant species effect in our analysis suggests that *P. bistorta* and *C. consimilis* were not different in their abilities to deter pikas with defensive compounds. Although our design did not allow us to test this hypothesis, independent feeding experiments at our site suggest that pikas actively avoided collecting *Festuca altaica* tillers containing alkaloid–based toxins but selected tillers without toxins (S. Koh and D.S. Hik, unpublished data). Therefore, pikas may make some intra-specific foraging decisions based on secondary defense compounds similar to other herbivores (e.g., Moore and Foley 2005). Fertilization, however, may affect the plant in more ways than simply increasing crude protein levels. The carbon – nutrient hypothesis (Bryant et al. 1983), for example, predicts a decrease in carbon-based defense compounds with increasing nitrogen.

In conclusion, we have experimentally demonstrated that pikas make more complex foraging decisions than previously reported. We also provide the first report of pikas making intra-specific foraging choices based on variation in nitrogen and water content in addition to species-specific selection criteria. Our results imply that tests of foraging theory may need to consider intra-specific forage characteristics because inter-specific ranking of forage species may vary based on intra-specific characteristics.

Table 3-1: Analysis of variance examining the effects of forage species, nitrogen content, and water content on forage selection by twenty-seven haying pikas according to a randomized block experimental design in which blocks were defined as individual pikas.

Source	df	SS	MS	F	*P*
Block	26	6.81	0.26	3.12	<0.001
Species (S)	1	0.16	0.16	1.96	0.164
Fertilizer (F)	1	0.13	0.13	1.59	0.209
Water (W)	1	0.05	0.05	0.58	0.447
S × F	1	0.09	0.09	1.06	0.305
S × W	1	0.01	0.01	0.16	0.689
F × W	1	0.12	0.12	1.50	0.223
S × F × W	1	0.33	0.33	4.01	0.047
Residuals	182	14.94	0.08		

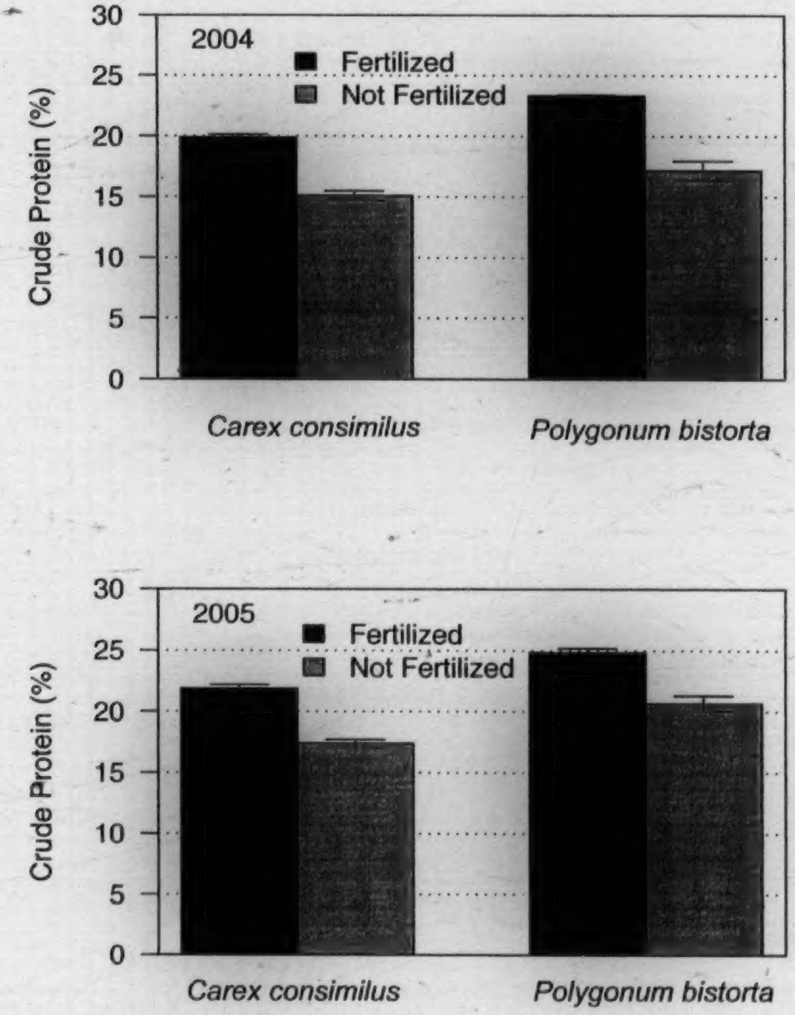

Figure 3-1: Effect of NPK fertilizer on the crude protein content of *P. bistorta* and *C. consimilis* during 2004 and 2005. Bars represent means ± 1 standard error.

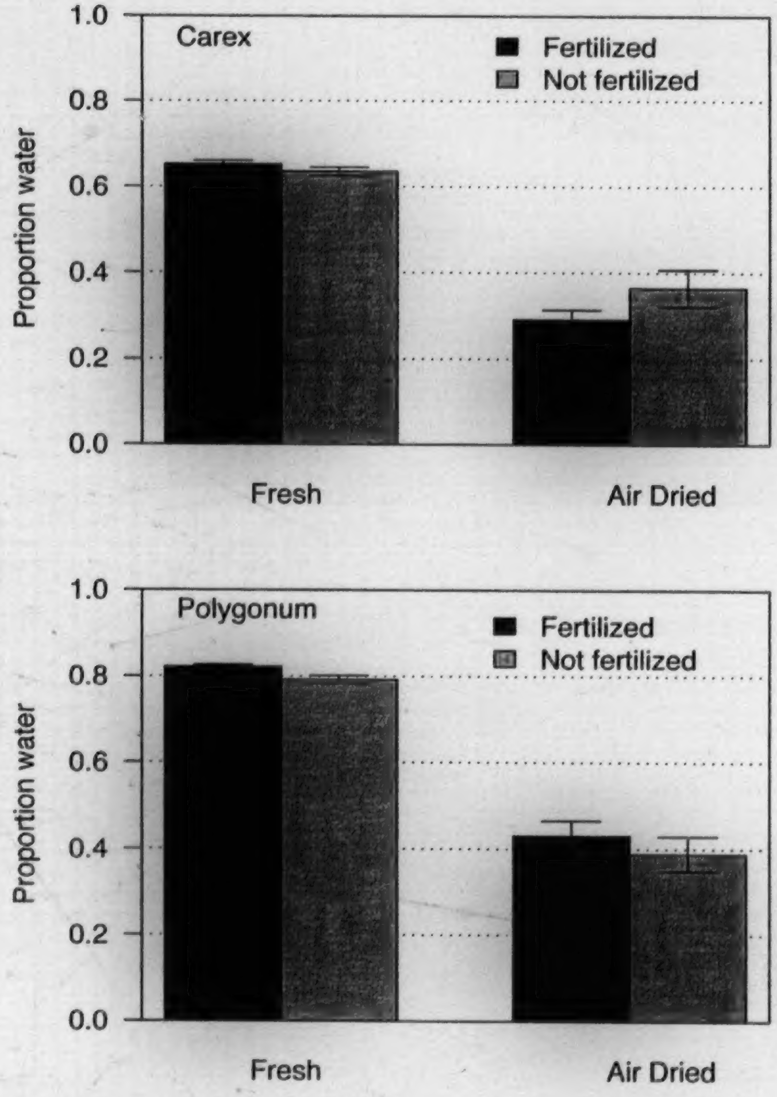

Figure 3-2: Proportional water content (proportion of total fresh mass that is water) for fresh and air dried plant specimens stratified by NPK fertilizer treatment for *C. consimilis* and *P. bistorta*. Bars represent means ± 1 standard error.

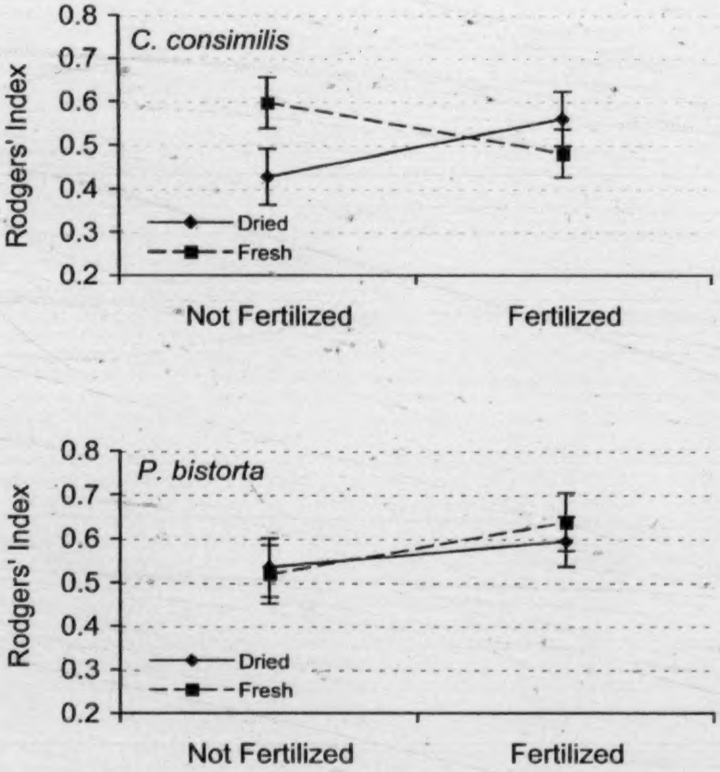

Figure 3-3: Selection of *C. consimilis* and *P. bistorta* with respect to water (fresh or dried) and nitrogen (fertilized or not) content by haying collared pikas. Values are mean Rodgers' Indices ± 1 standard error.

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CHAPTER 4: PIKA FOOD-CACHING: BET-HEDGING OR SOLE SOURCE OF WINTER FORAGE?

Introduction

Animals cache or hoard food in an attempt to control availability and quality during times of food scarcity (Vander Wall 1990). In most seasonal environments, food is abundant during the growing season, but relatively scarce or of poor quality during the non-growing season (Owen-Smith 2002). For many herbivores, plant protein is higher at the beginning of the growing season and declines as plants reach maturity (e.g., Millar 1971, Sinclair 1975, Greenwood and Barnes 1978). Caching allows animals to partially escape the potentially adverse consequences of forage scarcity, and may have implications for fitness by influencing survival (Rusch and Reeder 1978, Stacey and Ligon 1987, Wauters et al. 1995), body mass (Rusch and Reeder 1978, Buck and Barnes 1999), and weaning rates (Wauters et al. 1995). Long-term caching is a common behaviour for several northern herbivores such as red squirrels (*Tamiasciurus hudsonicus*; Hurly and Robertson (1990)), collared pikas (*Ochotona collaris*; MacDonald and Jones (1987)), voles (*Microtus* and *Clethrionomys*; Vander Wall (1990), and Arctic ground squirrels (*Spermophilus parryii*; Buck and Barnes (1999), Gillis et al. (2005)), presumably because of the relatively short growing season at high latitudes.

The caching behaviour of pikas has been well documented (Broadbooks 1965, Krear 1965, Millar and Zwickel 1972, Barash 1973, Conner 1983). Pikas collect and store large amounts of vegetation in caches, also known as haypiles, for consumption during winter. Pikas in North America (*O. princeps* and *O. collaris*) are asocial and each individual accumulates and defends a haypile for personal use (Millar 1971, Smith and Ivins 1984, Smith et al. 1990). Haypile location within a territory generally remains consistent across years (Broadbooks 1965). Pika haypiles may be used by other herbivores as a source of forage during winter (Smith et al. 1990), and infrequently exploited by neighboring pikas during summer to supplement their respective haypiles (Mckechnie et al. 1994).

Despite being well documented, the functional role of haypiles remains uncertain. Connor (1983) proposed that American pikas (*O. princeps*) in Colorado used haypiles as a 'bet hedging' strategy against inclement weather that would extend snow-cover and delay vegetation growth during spring. Excavation of haypiles by Millar and Zwickel (1972) in Alberta indicated that haypiles were not sufficiently large to be the sole supply of winter food. Dearing (1997b), however, argued that Millar and Zwickel (1972) underestimated haypile mass because of difficulties in extracting all vegetation from the many deep crevices within boulderfields. Using time-budget data, Dearing (1997b) reported that pikas in Colorado collected sufficient vegetation to sustain themselves during an entire winter, and that haypiles were more than a 'bet hedging' strategy.

Within this context, we examined the hypothesis that collared pika (*O. collaris*) haypiles are sufficiently large to serve as the sole source of food during winter. We measured 1) rates of vegetation delivery to haypiles throughout the entire 24-hr day, and 2) the amount of vegetation delivered per haying trip to estimate haypile mass. Further, we compared haypile mass estimates based on food delivery rates with empirical data from excavated haypiles. We also documented interactions between pikas and hoary marmots (*Marmota caligata*) and arctic ground squirrels at haypiles.

Methods

STUDY AREA

The study was conducted in a 4-km^2 alpine valley within the Ruby Range, east of Kluane Lake, Yukon, Canada (61°13' N, 138°16' W; 1600-2200 a.s.l). The valley was a mosaic of meadow and tundra vegetation interspersed with patches of boulderfields (pika habitat). Vegetation communities were dominated by *Dryas octopetala*, *Salix* spp. *Cassiope tetragona* and several graminoids (*e.g., Carex consimilis*) (Hik et al. 2001, McIntire and Hik 2005). Collared pikas, hoary marmots (*Marmota caligata*) and arctic ground squirrels were the dominant mammalian herbivores.

HAYING RATES

We used two Sentinal™ video cameras (Models HWB-2 5A6 and AC 2002-1, Sandpiper Technologies, Manteca, CA) to record the rate at which pikas delivered vegetation to their haypile, measured as the number of trips per hour. Only actively haying pikas were selected for observation. For each recording session one camera was deployed per haypile allowing us to simultaneously record activity within two pika territories. Cameras were placed at vantage points where movements of pikas to and from the haypiles were easily detected. Cameras were programmed to record images at a rate of 2.5 frames per second throughout the entire 24-hr period. Because of the high-latitude of our site there was adequate ambient light to record nighttime activity during June. However, nighttime darkness (1 – 4 h) in July and August limited our data collection to one camera that was equipped with 12 onboard infrared lights and a day-night sensor (Model AC 2002-1). The infrared lights illuminated an area within 3-4m of the camera, and we therefore positioned the camera accordingly.

LOAD SIZE

Pikas are classical multiple prey loaders (Stephens and Krebs 1986), such that they collect multiple parts of several plant species during each haying trip. These loads were deposited on the haypile as discrete bundles and churned into the haypile over time through the movements of the pika. We regularly inspected active haypiles and opportunistically collected deposited loads before they had been mixed into the rest of the haypile. Loads were oven-dried and weighed to the nearest 0.1g.

HAYPILE MASS VIA SIMULATIONS AND EXCAVATIONS

For the months of June, July and August we simulated haypile mass by randomly selecting, with replacement, an hourly haying rate and a load size (dry mass) in order to calculate the mass of vegetation delivered to the haypile each day [Eqn 1]. Haying at our site began approximately mid-June and continued to mid-September. We assumed that haying activity in early September did not differ from August. Accumulated mass per day was converted to mass per month by multiplying by 15, 31, 31, and 15 days for June, July, August, and September, respectively. Total summer mass (dry mass) was the sum of the four monthly estimates.

[Eqn 1]

$$\frac{mass}{day} = \frac{trips}{hr} \cdot \frac{mass}{trip} \cdot \frac{24\,hrs}{day}$$

In mid-September 2006, all visible and accessible vegetation was excavated from 27 pika haypiles, placed in large plastic bags, and weighed to the nearest 100g. All vegetation was returned to the haypiles following weighing.

ESTIMATION OF FOOD RESERVES

We estimated food reserves as haypile mass divided by the daily consumption rates obtained from the literature (Johnson and Maxwell 1966, Millar and Zwickel 1972, Dearing 1997b, 1997a; Table 4-1). Dearing (1997b, 1997a) and Millar and Zwickel (1972) used captive *O. princeps* provided with a known amount of haypile material to estimate daily consumption rates. Johnson and Maxwell (1966) used allometric scaling and energetic data collected from the stomach and fecal material of harvested *O. princeps* to estimate the daily consumption rate. Their estimate of 50.4 kcal/day assumed a 171 g pika body mass, so therefore we recalculated the consumption rate for a 157g adult pika, the mean body mass for *O. collaris* at our site (Franken and Hik 2004), to be 47.2 kcal/day. Assuming haypile vegetation provided 4.5 kcal/g (Johnson and Maxwell 1966), pikas requiring 47.2 kcal/day would need to consume 10.5 g/day (47.2 kcal/day ÷ 4.5 kcal/g) of haypile vegetation.

Results

SAMPLE SIZE AND GENERAL OBSERVATIONS

We obtained 220, 282, and 294 hours of video data for June, July, and August, on 7, 6, and 5 individual pikas, respectively. Mammalian predators (e.g., weasels (*Mustela* spp.) or red foxes (*Vulpes vulpes*)) were never observed at haypiles. Hoary marmots, arctic ground squirrels, and ptarmigan (*Lagopus* spp.) broods were observed in the vicinity of haypiles, but at no time did any of these species forage from haypiles or have direct interactions with pikas. Pikas deposited vegetation directly onto the surface of the haypile with no apparent attempt to air dry plants prior to storage.

HAYING RATES, LOAD SIZE, AND DAILY ACTIVITY

Pikas actively collected vegetation for haypiles throughout the entire 24-hr day although peaks of activity were noted (Figure 4-1). Haying rates in June appeared to peak twice daily at approximately 0500 – 0900 hrs and again at 2100 – 2400 hrs. Similar peaks of activity were less obvious in July and August although haying seemed to be more common at 0600 - 1300 and 2000 - 2300. The mean haying rate per hour increased monthly from 3.7 ± 0.7 (95% CI, n = 223) trips in June, 5.0 ± 0.5 (95% CI, n = 283) trips in July, and 6.6 ± 0.8 (95% CI, n = 307) trips in August. The maximum rate did not appear to vary monthly, but the amount of mid-day activity increased sharply during July and August relative to June (Figure 4-1). Haying activity was reduced between 0100 – 0400 hrs for all months, however pikas were occasionally observed haying during these hours. Pikas at our site made 93.0 ± 14.8 ($\bar{x}$ ± s.e.), 113.1 ± 12.5, and 146.9 ± 16.4 haying trips per day for June, July and August, respectively. Assuming the activity rate in September was similar to August this represents a total of 11, 660 haying trips from 15 June to 15 September. Pikas carried an average of 0.62 ± 0.06 g (95% CI, range = 0.01 - 3.77 g, n = 213) of vegetation per haying trip (Figure 4-2A).

HAYPILE MASS VIA SIMULATIONS AND EXCAVATIONS

Our simulations provided estimates of median haypile mass (dry weight) by mid-September of 5.5 kg (25th and 75th quantiles = 2.8 and 9.8 kg, respectively; mean = 7.4 kg; Figure 4-2B). Mean haypile mass based on the excavation of 27 pika haypiles in mid-September 2006 was estimated to be 3.1 ± 0.82 kg (95% CI, n = 27).

ESTIMATED FOOD RESERVES

The amount of food represented by the median 5.5 kg haypile differed according to consumption rate (Figure 4-3). However, for all four consumption rates, at least 75% of simulated haypiles had a minimum of 90 days (3 months) of food reserves and 50% of simulated haypiles had a minimum of 177 days (5.9 months) of food reserves by mid-September. Dearing (1997b) and Millar and Zwickel (1972) based their consumption rates on feeding trials and therefore these are likely the most reliable estimates. Based on Dearing's (1997b) estimate, the median haypile at our site had 251 days (8.3 months) of vegetation based a 22 g/day rate of consumption (Dearing 1997a). Pikas had a median of 178 days (5.9 months) of food based on Millar and Zwickel's (1972) maximum estimate of 31 g/day and 527 days (17.6 months) of food using Johnson and Maxwell's (1966) consumption estimate (Figure 4-3).

Discussion

Haypiles mass based on simulations (median = 5.5 kg) and excavations (median = 2.2 kg, weighted mean = 3.1kg) were similar to masses based on excavations reported for *O. princeps* (5.7 - 7.7 kg by Dearing (1997b), 4.8 kg by Sundby (2002), and 0.4 - 6.0 kg by Millar (1971)) and *O. rufescens* (5 kg in Smith et al. 1990). Millar (1971) further reported differences among sex and age classes in which adult males had larger haypiles (2.9 ± 0.3 kg) by the end of September than adult females (2.0 ± 0.3 kg). Juveniles, in turn, had significantly smaller haypiles (1.1 ± 0.2 kg) than adult females.

Collared pikas at our site tended to make more haying trips in the early morning and again from 2100 – 2300 during June, similar to the patterns described for *O. himalayana* (Smith et al. 1990) and *O. princeps* (Severaid 1950). Pikas increased their haying rate in July and August by increasing their midday activity such that peak activity times became less obvious. Broadbooks (1965) also noted that *O. collaris* was actively haying throughout the day with no major lulls in midday activity. Activity was reduced considerably from 2400 – 0400 in all months, however pikas were observed haying during these times. Therefore it cannot be assumed that pikas are inactive during these times and time budgets should be based on the entire 24-hr period to capture the full range of behaviours. Smith (1974) reported elevation differences in the daily activity of *O. princeps* and attributed the increased levels of nocturnal activity at lower-elevations due to higher daytime temperatures that restricted activity. We hesitate to attribute nocturnal activity to inhospitable daytime temperatures because pikas also were more active during the day than at night. Rather, nocturnal activity could be due to atypical circadian rhythms recently discovered in high-latitude reindeer (*Rangifer tarandus*; van Oort et al. 2005), or a relatively shorter growing season that forces pikas to harvest at a maximum rate to obtain enough vegetation for their haypiles.

Collared pikas at our site carried less vegetation (by mass) per haying trip than reported for *O. princeps* (Dearing 1997b). The reasons for this are unknown, but likely reflect differences in plant species composition and plant morphology. Vegetation carried by haying pikas typically extends out of both sides of their mouth, enabling them to carry multiple stems simultaneously (i.e., multiple prey loaders; Stephens and Krebs 1986). In other words, they are less constrained by mouth volume than other herbivores. Plants in the subarctic Ruby Range meadows may be of smaller stature then plants in Rocky Mountain meadows where previous observations have been made (e.g. Dearing 1997b), requiring more trips to collect the same amount of cached vegetation.

We observed no instances of other vertebrate herbivores removing or disturbing haypile vegetation, suggesting that pikas were not directly affected by inter-specific competition. Both hoary marmots and Arctic ground squirrels, the other abundant mammalian herbivores at our site (Hik et al. 2001), hibernate from September to April (Gillis 2003) and are therefore unable to consume haypile vegetation during winter. Local distributions of smaller mammals such as voles (*Clethrionomys* spp.) and shrews (*Sorex* spp.) have been reported to be associated with *O. alpine, O. rutila* and *O. hyperborea* haypiles (Smith et al. 1990), however we did not observe any voles, shrews, or other small mammal activity in our video data. It is possible that these species inconspicuously foraged at haypiles under the boulders, but we did not observe such activity. Larger herbivores such as caribou (*Rangifer tarandus*), snow sheep (*Ovis nivicola*) and elk (*Cervus elaphus*) are known to forage from *O. alpina* and *O. hyperborea* haypiles during winter snowstorms (Smith et al. 1990). Caribou and Dall sheep (*Ovis dalli*) are frequently observed at our alpine site, but have never been observed foraging from haypiles during summer. At our site, caribou move into forests at lower elevations during winter (Danby 1999). Dall sheep remain on south-facing alpine grassland areas (Hoefs and Brink 1978, Hoefs and Cowan 1979) and while unlikely, it is possible that they might occasionally forage from pika haypiles. However, this behaviour has never been observed.

Pikas at our site accumulated sufficient vegetation in haypiles to serve as a sole source of food for a median of 5.9 – 17.5 months, depending on the consumption rate used in these calculations. Millar and Zwickel (1972) concluded that *O. princeps* required 6kg by the end of September to survive six months, the mean length of the non-growing season in southern Alberta. Of 105 haypiles excavated at that site only 3 (2.9%) had ≥ 6kg and therefore insufficient vegetation to provide the sole source of winter nutrition. At our site, only 1 of 27 (3.7%) excavated haypiles had ≥ 6 kg of vegetation by mid-September when haying activity was largely completed. Excavated haypiles at our site were smaller than simulated haypiles. Haypile vegetation may be located out of reach within the talus and therefore haypile masses based on excavations are underestimates (Krear 1965, Dearing 1997b).

Pikas at our site forage in meadows outside of the growing season until snow cover greatly reduces accessibility (K. O'Donovan, unpublished observations) and therefore collared pikas are not completely reliant on their haypiles for the entire non-growing season. Snow cover at our site lasts approximately 6 - 7 months (Danby 2006) and therefore pikas appear to accumulate sufficient food reserves for this period, supporting Dearing's (1997b) argument that pikas collected sufficient haypile reserves to improve survival during winter. Foraging in meadows during the non-growing season may be a strategy to ensure sufficient reserves remain in the haypile for use when meadow vegetation is snow-covered.

Food hoarding, such as haying by pikas, provides a buffer against variable environmental conditions, and often is critical to a species' ability to maintain persistent populations in harsh environments (Vander Wall 1990). Haying also may confer a competitive advantage to pikas over other sympatric herbivores that store energy as body fat reserves for use during hibernation (such as hoary marmots or Arctic ground squirrels) because pikas are not affected by digestive constraints (such as passage time) at the time of collection. Further, the relocation of vegetation from the meadow to haypiles may enhance nutrient cycling (Aho et al. 1998), and alter plant species diversity (Huntly 1987, Roach et al. 2001). Therefore, the large amount of time spent haying each summer has implications for community interactions and biodiversity, as well as pika survival (Chapter 5).

Table 4-1: Number of days of food reserves contained within pika haypiles according to published estimates of consumption rates for pikas and assuming i) haypiles contain a median of 5.5 kg of vegetation by mid-September, ii) the mean body mass of a non-lactating *O. collaris* adult is 157 g (Franken and Hik 2004), and iii) the haypile energetic content is 4.5 kcal g^{-1} (Johnson and Maxwell 1966).

Consumption rate	Data Source	Source
22 g day^{-1}	Captive animals	(Dearing 1997b)
26-31 g day^{-1}	Captive animals	(Millar and Zwickel 1972)
47.2 kcal day^{-1} (10.5 g day^{-1})	Gut contents & energetics data, (modified for a 157 g adult)	(Johnson and Maxwell 1966)

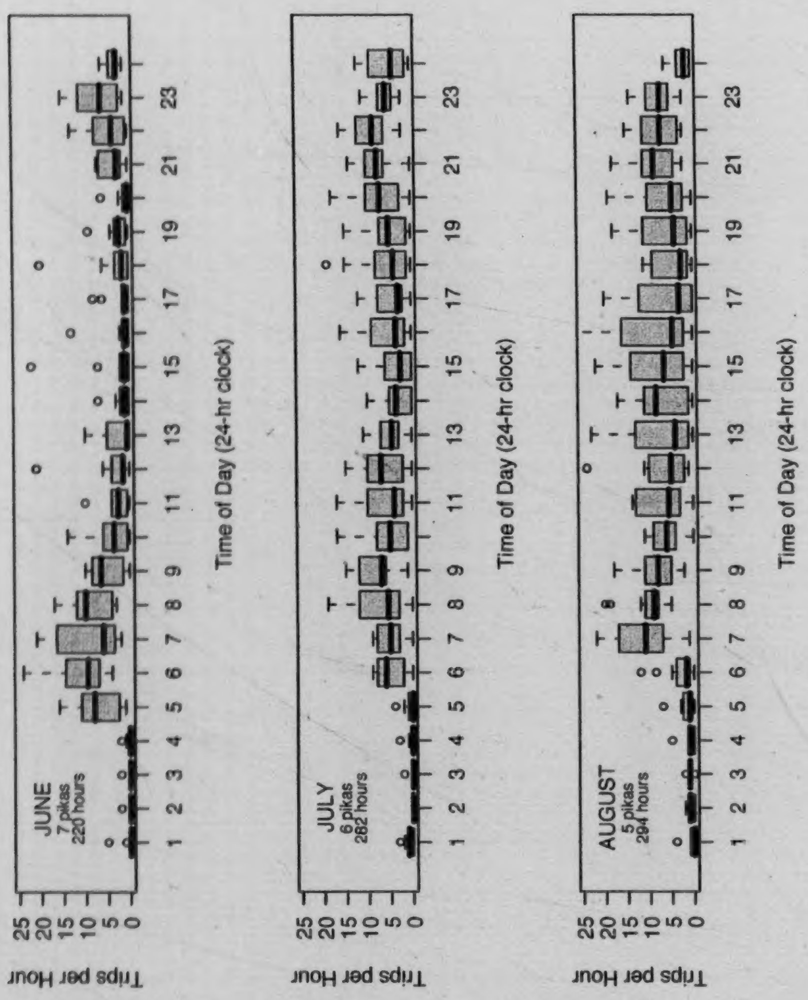

Figure 4-1: Number of vegetation deliveries to collared pika haypiles (trips per hr) according to month and time of day in southwest Yukon during 2005. For each boxplot, the horizontal line represents the median value, the top and bottom of each box indicates the 25th and 75th percentile, and the whiskers represent the 10th and 90th percentiles. The horizontal bars for each month indicate daylight hours.

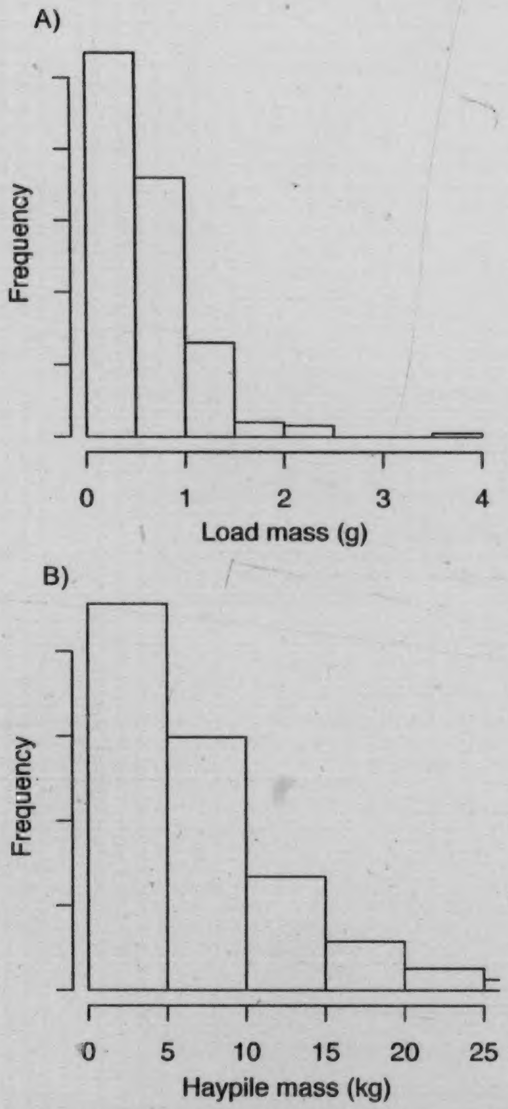

Figure 4-2: A) Vegetation mass (g) delivered per trip to haypiles by collared pikas, and B) estimated haypile mass (kg) by the end of August based on simulations using rates of delivery and mass of vegetation delivered per trip.

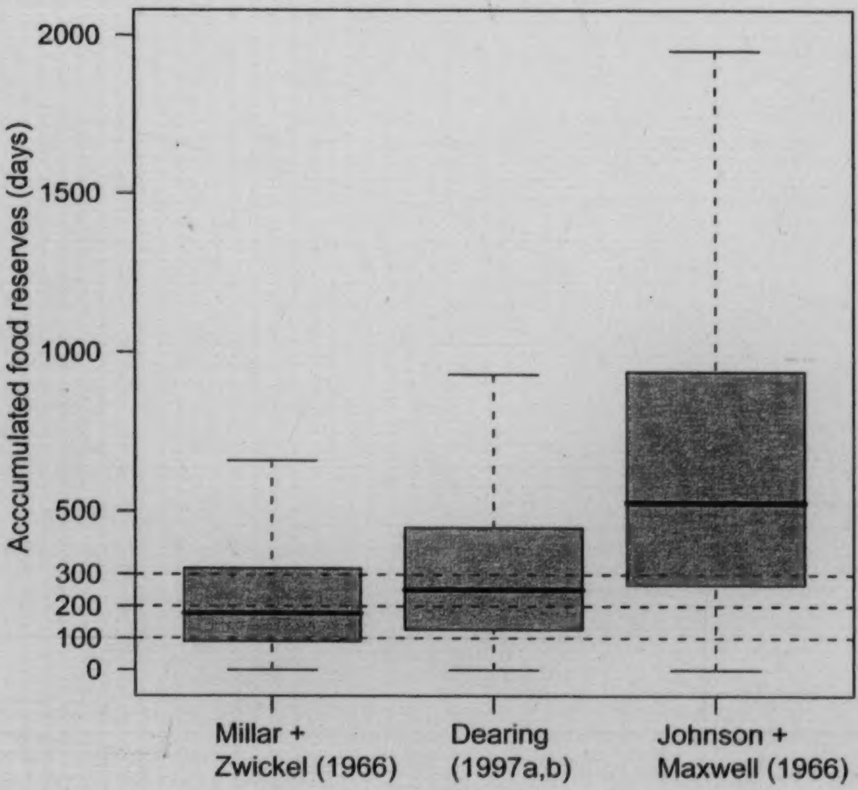

Figure 4-3: Number of days of vegetation contained within pika haypiles as estimated by delivery rates and load size for three published rates of consumption. For each box, the horizontal line represents the median value, the top and bottom of each box indicates the 25th and 75th percentile, and the whiskers represent the 10th and 90th percentiles.

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CHAPTER 5: SEASONAL ONSET OF FOOD HOARDING INFLUENCES THE OVER-WINTER SURVIVAL OF COLLARED PIKAS, *OCHOTONA COLLARIS*

Introduction

Food hoarding is an adaptive behaviour used to manage food availability through time and space (Andersson and Krebs 1978, Vander Wall 1990). For many species, food may become scarce or unavailable due to factors such as competition (Keddy 2001), seasonality (Owen-Smith 2002), or perceived risk of predation (Hik 1995, Morrison et al. 2004). In such situations, a food cache allows individuals to meet their nutritional requirements despite unfavorable conditions (Vander Wall 1990).

Hoarding patterns vary inter-specifically such that food may be stored for as little as a few minutes (Brodin and Ekman 1994) to several years, and may be located at many (scatter-hoarding) or few (larder hoarding) sites (Vander Wall 1990). Further, the cache may form all (e.g., honeybees, *Apis mellifera;* (Owens 1971) or only a portion (e.g., coyotes, *Canis latrans,* O'Donahue (1998), Arctic ground squirrels, *Spermophilus parryii,* Gillis et al. (2005)) of the required nutrition during periods of food scarcity.

The ability to maintain adequate nutritional levels (e.g., energy, protein, etc.) has important fitness benefits such as increased survival (Rusch and Reeder 1978, Stacey and Ligon 1987, Wauters et al. 1995), post-winter body mass (Rusch and Reeder 1978, Buck and Barnes 1999), timing of breeding (King 1983, Koenig and Mumme 1987), pregnancy rates (Gashwiler 1979), and weaning rates (Korpimäki 1987). Even relatively small hoards that supply only a portion of the individual's energetic needs can have important influences on survival (Hitchcock and Houston 1994).

Hoarding behaviour may be influenced by a variety of factors including genetics, reproductive status, food deprivation, gender, photoperiod, temperature, and the amount of food already collected (Vander Wall 1990). For herbivores in strongly seasonal environments, where summer growing seasons are short relative to winter, the initiation of hoarding is likely determined by vegetation phenology and moisture content (Smith 1974). Under such conditions, an earlier start to hoarding should increase the amount of vegetation stored for winter. If a cache represents most of an individual's winter food reserves, then an earlier start should translate into improved survival, and therefore, increased fitness.

In this study, I examined the seasonal timing of hoarding behaviour, also known as 'haying', of a small (~160 g) alpine lagomorph, the collared pika (*Ochotona collaris*), and subsequent over-winter survival. The haying behaviours of collared pikas and the closely related American pika (*O. princeps*) are well documented (Broadbooks 1965, Krear 1965, Millar and Zwickel 1972, Barash 1973, Conner 1983, Huntly et al. 1986, Dearing 1996). Briefly, *O. collaris and O. princeps* individuals make thousands of foraging trips each summer to accumulate large amounts of vegetation in haypiles for consumption during winter (5.7 - 7.7 kg for *O. princeps*, Dearing (1997) and approximately 5.5 kg for *O. collaris*, Chapter 4). Each pika defends a haypile for its personal use (Smith and Ivins 1984, Smith et al. 1990). The timing of when pikas begin haying each summer appears to be a function of vegetation maturity and moisture content (Smith 1974, Smith and Weston 1990). Earlier snowmelt in spring should advance vegetation phenology and allow pikas to accumulate greater amounts of vegetation relative to springs with delayed snowmelt. The initiation of haying may also vary by age and sex such that adult males begin haying prior to adult females, and juveniles are delayed relative to adults and therefore have less time to accumulate vegetation for haypiles (Millar 1971, Smith 1974, Smith and Ivins 1984, Huntly et al. 1986).

The ecological significance of haypiles has been the subject of some debate (Dearing 1997). Both Connor (1983) and Millar (1972) reported that haypiles did not contain sufficient vegetation to be the sole source of winter food and concluded that haying activity was a 'bet hedging' strategy to be used during inclement weather or delayed snow melt in spring. Other studies have reached the opposite conclusion (e.g., Dearing (1997)). Millar (1971) reported that haypile mass had no effect on *O. princeps* reproduction and supplementing haypiles with 1kg of vegetation did not affect subsequent weaning rates in the following spring. Kreuzer and Huntly (2003) studied *O. princeps* population demographics in Colorado and concluded that birth rates and survivals were strongly associated with the timing of snowmelt such that areas with delayed snowmelt were sink populations. We are unaware of any study that examined the relationship between the timing of haying behaviour and subsequent over-winter survival of pikas.

In this study we tested two main hypotheses. First, we tested whether the timing of hoarding behaviour was age- and sex-dependant. Based on Millar (1971), Smith (1974), Smith and Ivins (1984), and Huntly (1986) we predicted that 1) adult pikas would initiate haying earlier than juveniles, and 2) adult males would begin haying prior to adult females. Second, we tested the hypothesis that earlier initiation of hoarding behaviour improves over-winter survival. We predicted over-winter survival would be positively affected by earlier initiation of haying behaviour.

Methods

STUDY AREA

The study was conducted in a 4-km^2 alpine valley within the Ruby Range, east of Kluane Lake, Yukon, Canada (61°13' N, 138°16' W; 1600-2200 a.s.l). The valley was a mosaic of meadow and tundra vegetation interspersed with patches of boulderfields (pika habitat). Vegetation communities were dominated by *Dryas octopetala*, *Salix* spp. *Cassiope tetragona* and several graminoids (e.g., *Carex consimilis*) (Hik et al. 2001, McIntire and Hik 2005). Collared pikas, hoary marmots (*Marmota caligata*) and Arctic ground squirrels (*Spermophilus parryii*) were the dominant mammalian herbivores.

DETERMINING THE START OF HAYING ACTIVITY

Since 1995, each haypile within our study site has been marked with a wooden stake so all likely haypile locations were known. These haypile locations were checked weekly from mid-June to mid-August during summers of 2004 and 2005 for the presence of freshly collec[illegible]getation that indicated the initiation of haying activity for that year. Freshly collected vegetation was easily distinguishable from brown and decomposing vegetation collected during previous years.

SURVIVAL

We monitored the fates (lived or died) of all individuals for which we knew the date of haypile initiation (i.e., those pikas listed in Table 5-1). As part of a long-term study of pika ecology (Franken and Hik 2004a, Morrison and Hik 2006), pikas were captured each summer using Tomahawk live-traps baited with fresh native vegetation. Individuals trapped for the first time were marked with numbered metal ear tags (Monel #1) and a unique color combination of thin wire to allow for later re-identification. We followed Duke (1951) in assigning gender and classified individuals as juveniles or adults based on body mass and molt pattern (Franken and Hik 2004b).

Because of their high visibility (Smith 1974, 1980), extreme adult philopatry (Smith and Ivins 1983), and data from our site indicating the recapture probability was approximately one (Chapter 6), we did not have to account for overlooked individuals when determining survival.

STATISTICAL ANALYSES

We used a three-way analysis of variance (ANOVA) to examine the effects of pika age, pika sex, and year on the timing of haying behaviour initiation. Age was classified as either juvenile or adult, sex was classified as male or female, and year was either 2004 or 2005. The response variable was the day of year when haypile accumulation began (e.g., Day 1 = January 1st). Age, sex, and year were treated as fixed effects.

We used classification trees (Breiman et al. 1984) to model pika over-winter survival (survived or died) as a function of pika age (juvenile or adult), year (2004 or 2005), sex, and when haying behaviour was initiated in the preceding summer measured as the day of year (i.e., Day 1 = January 1st). Classification trees are becoming increasingly common for addressing a variety of ecological issues such as predicting species occurrence (De'ath and Fabricius 2000, Morrison et al. 2003), age classification (Karels et al. 2004), survival (Franken 2002), and the response of populations to climate variability (Crozier and Zabel 2006).

The theory and details of implementing classification trees are well described elsewhere (Breiman et al. 1984, Faraway 2006). Briefly, classification trees are a regression technique that allows the use of categorical and continuous data, non-linear relationships, missing values, and implicitly include interactions among predictor variables (Faraway 2006). Trees are created using recursive partitioning to separate the response observations into increasingly homogenous subsets. Each split (node) in the tree is based on a threshold value of the predictor variable that produces the greatest within-group similarity for the response variable. The entire dataset may be partitioned until each observation is explained or according to pre-specified stopping criteria. The optimal tree size (i.e., number of nodes) is a balance between explanatory ability and generality to other datasets. We determined the optimal tree size through a k-folds cross-validation pruning procedure as described by Faraway (2006). We measured the ability of the pruned tree to predict known observations and calculated misclassification rates accordingly.

Results

HAYPILE MONITORING

We monitored pika haypiles from 11 June (Day 162) to 14 August (Day 226) in 2004 and 22 June (Day 173) to 20 August (Day 232) in 2005. The number of active haypiles at the start of our monitoring period did not appear to differ between years (Figure 5-1). Therefore, annual differences cannot be attributed to variation in our monitoring protocol. Weekly monitoring allowed us to determine the annual onset of haying for 44 pikas in 2004 and 64 pikas in 2005 (Table 5-1).

EFFECTS OF AGE, SEX, AND YEAR ON ONSET OF HAYING

There was no 3-way interaction of age, sex, and year ($F_{1,88} = 1.40$, $P = 0.24$; Table 5-2), allowing us to consider 2-way interactions. Haypile initiation was significantly related to an age x year interaction ($F_{1,88} = 6.80$, $P = 0.011$; Table 5-2) in which adult pikas began haying an average of 16 days earlier in 2004 (mean day of year = 183.3 ± 4.4) relative to 2005 (199.3 ± 2.5) (Figure 5-2). There were no annual differences observed for juveniles (Figure 5-2), and juveniles in 2004 lagged behind adults for the entire monitoring period (Figure 5-1). However, in 2005, juveniles initially lagged behind adults, but had caught up by the end of July (Figure 5-1). The influence of sex was inconclusive (day of year = 201.5 ± 2.2 days for males and 196.4 ± 2.8 for females; $F_{1,88} = 3.34$, $P = 0.071$).

EFFECTS OF AGE, SEX, YEAR, AND HAYING ONSET ON SURVIVAL

Classification tree analysis using year, age, sex, and day of year as predictor variables, indicated that survival was greatest for pikas in 2005 when they began haying prior to day 213 (July 31st) (Figure 5-3). Over-winter survival during 2004-05 was less than half that observed in 2005-06 (25% survival in 2004-05 (n = 44), and 56% survival in 2005-06, n = 64)). Haying dates in 2004 and pika age did not appear in the pruned tree suggesting that neither influenced survival in that year. The pruned tree correctly classified 67.2% of known deaths and 70.2% of known survival events for an overall misclassification rate of 31.5%.

PARTURITION DATE

In a post-hoc analysis, we used the Gompertz growth equation (Ricklefs 1967) parameterized for juvenile collared pikas at our study site by Franken and Hik (2004b) to estimate parturition dates for the years of our study (i.e., 2004 and 2005). Mean parturition date did not appreciably differ among years (June 7th in 2004 and June 9th in 2005).

Discussion

Our study evaluated the factors affecting when pikas began hoarding vegetation for winter consumption and its effect on subsequent survival. Our results suggested that the annual onset of haying behaviour was related to an interaction between pika age and year. Juveniles did not vary in their onset of haying behaviour, however adults started haying 16 days earlier in 2005 than in 2004. Similar age-specific patterns were observed by Krear (1965) and Millar (1971).

Parturition varied annually at our site such that years of later parturition were associated with greater snow accumulation during the preceeding winter and the timing of snowmelt in spring (Franken and Hik 2004b). A late spring, therefore, would result in delayed juvenile dispersal, territory acquisition, and accumulation of haypile vegetation. Mean parturition date did not appreciably differ among years (June 7th in 2004 and June 9th in 2005), and may explain why juveniles did not differ annually in the timing of haying behaviour.

Because adult females must nurse their young, and therefore have greater time and energetic constraints relative to adult males, we expected adult females to start haying later than adult males (i.e., a significant age × sex interaction) as reported by Millar (1971). However, we observed no sex-based differences among adults. A lack of difference may be because 1) the time and energetic costs of nursing and tending offspring on adult females are reduced or absent before haying begins for adult males and therefore both sexes have approximately equal opportunity to begin haying, or 2) adults females compensate by increasing haying effort following weaning of offspring.

The hypothesis that over-winter survival was related to the timing of haying behaviour was supported. The effect of this timing, however, was conditional on the year of observation and the age of the individual. The 2005 date threshold (Day 213 or July 31st) selected by the classification tree analysis closely corresponded to the date juveniles and adults had approximately the same cumulative percentage of active haypiles. In 2004, and before July 31st in 2005, juveniles lagged behind adults in the initiation of haypile activity. However, by July 31st 2005, adults and juveniles had approximately the same proportion of active haypiles. In some years, therefore, juveniles appear able to emerge from the natal nest, disperse, find and claim a vacant territory, achieve adult body mass, and begin haying without any delay relative to adults. Earlier haying did not affect over-winter survival in 2004-05 suggesting that, in some years, other factors may over-ride the amount of vegetation contained within a haypile. For example, mid-winter freeze-thaw events may have important effects on pika survival that are independent of food reserves (Smith et al. 2004).

Peak vegetation biomass near talus occurs in late July at our site and senescence begins soon thereafter (McIntire and Hik 2005). Thus, pikas that begin haying in late July have access to maximum vegetation biomass and can therefore quickly accumulate vegetation for haypiles. However, in doing so, they also assume the risk of collecting vegetation of steadily declining biomass (McIntire and Hik 2005) and quality (Millar 1971). Therefore, starting late in the season will affect both the amount and quality of vegetation contained within haypiles and may affect pika nutrition during winter with implications for survival.

Much of the annual variation in population growth rate at our site can be attributed to the survival of adult females (Chapter 6). Adult survival, in turn, was strongly correlated to the Pacific Decadal Oscillation during the previous winter (i.e., a 1-year time lag). The underlying mechanism by which the lagged PDO appears to be through its affects on the timing of spring snowmelt (Chapter 6).

Therefore, earlier growing seasons may allow pikas to begin haying earlier and therefore improve subsequent over-winter survival.

The timing of parturition may affect survival in that individuals born earlier in a summer are expected to have better over-winter survival (Roff 1992, Gillis 1998). However, over-winter survival of juveniles at our site was unaffected by parturition date because their rapid growth rate allowed most individuals to achieve adult mass before winter despite date of parturition (Franken and Hik 2004b).

To conclude, the day of year that pikas begin haying varied between years for adults but not for juveniles. The survival benefits of earlier accumulation of vegetation also varied between years. Therefore, the factors influencing pika behaviour and survival are not consistent over time. Increased variability in spring snowmelt patterns, as predicted to occur due to global climate change (IPCC 2001, ACIA 2005) could have important implications for the population dynamics of alpine mammals, like pikas, whose survival partially depends on their ability to acquire food resources for use during winter.

Table 5-1: Number of active pika haypiles for which the date of haypile initiation is known. Haypiles were stratified by year and the sex and age of the resident pika.

Sex-Age Class	2004	2005	Total
Males	15	28	43
Juveniles	9	12	21
Adults	6	16	22
Females	22	31	53
Juveniles	12	10	22
Adults	10	21	31
Unknown sex	7	5	12
Juveniles	6	1	7
Adults	1	4	5
Total	44	64	108

Table 5-2: Three-way analysis of variance (ANOVA) for the effects of collared pika age (adult or juvenile) and sex (male or female), and year (2004 or 2005) on the day of haypile initiation in the southwest Yukon. Sex, age, and year were treated as fixed factors.

Source	df	F	*P*
Age	1	10.17	0.002
Sex	1	3.34	0.071
Year	1	6.59	0.012
Age × Sex	1	0.21	0.647
Age × Year	1	6.80	0.011
Sex × Year	1	0.26	0.610
Age × Sex × Year	1	1.40	0.240
Residuals	88		

Table 5-3: Mean (± standard error) day of year (i.e., Day 1 = January 1st) when pikas initiated haying behaviour, stratified by sex, age, and year.

Sex-Age Class	2004	2005	Years Pooled
Males	198.4 (3.9)	203.7 (2.5)	201.5 (2.2)
Juveniles	206.0 (4.2)	207.8 (3.1)	206.8 (2.6)
Adults	189.2 (6.1)	201.8 (3.4)	197.7 (3.2)
Females	191.7 (6.0)	198.9 (2.9)	196.4 (2.8
Juveniles	204.4 (6.6)	201.7 (3.5)	202.9 (3.4)
Adults	172.7 (5.3)	196.8 (4.4)	190.2 (4.2)
Sex-Age Pooled	196.8 (3.0)	200.9 (1.8)	199.3 (1.6)

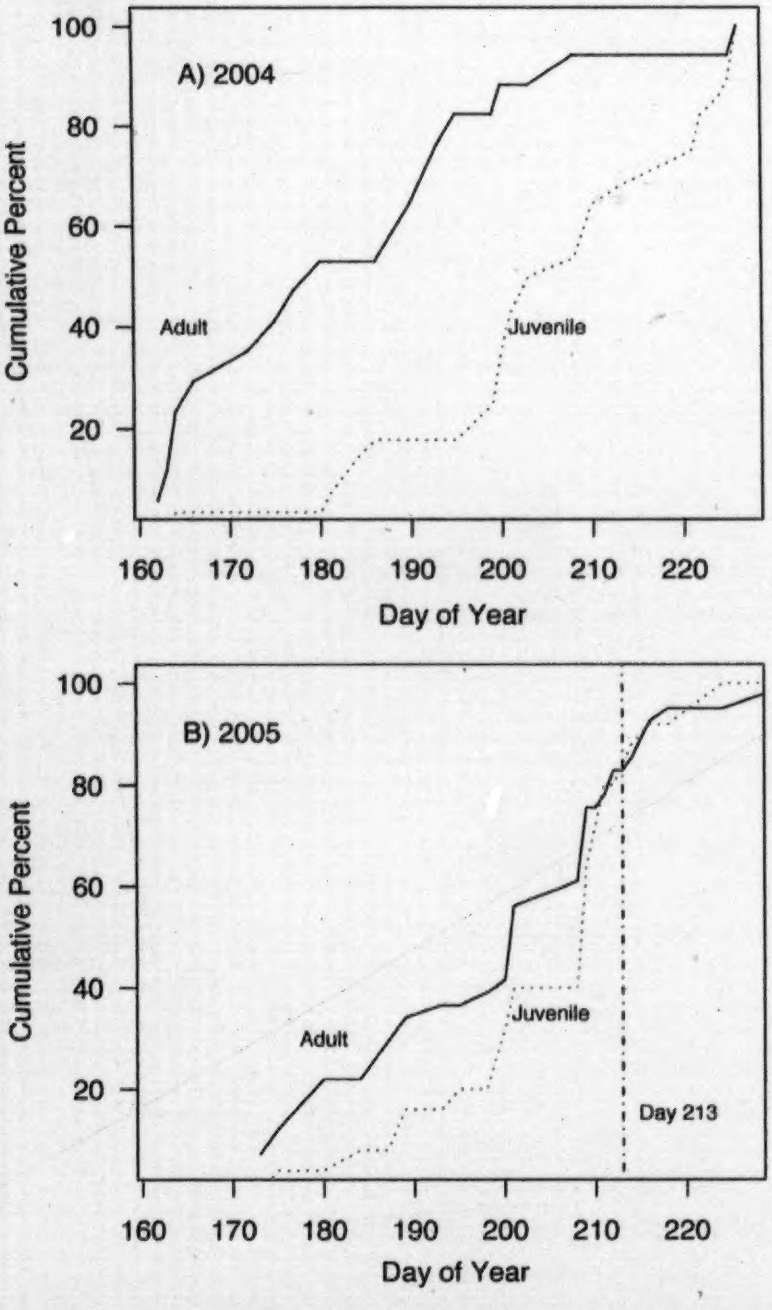

Figure 5-1: Cumulative percentage of active haypiles throughout a summer growing season stratified by year (2004 and 2005) and age. Solid lines represent adult pikas, and dotted lines represent juveniles. Day of year is the number of days elapsed since January 1 of a given year.

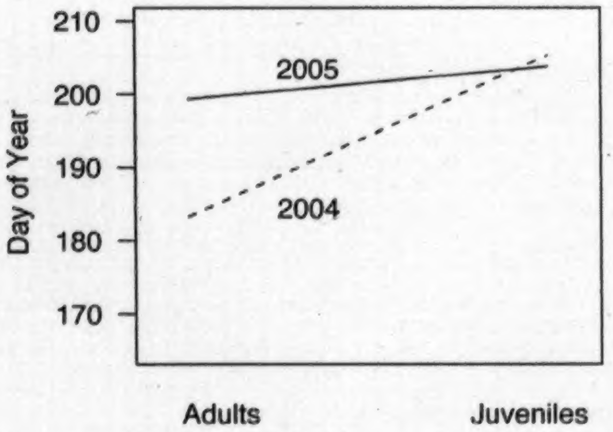

Figure 5-2: Interaction of pika age and year on the initiation of haying behaviour measured as mean day of year (Day 1 = January 1st) in 2004 (dotted line) and 2005 (solid line).

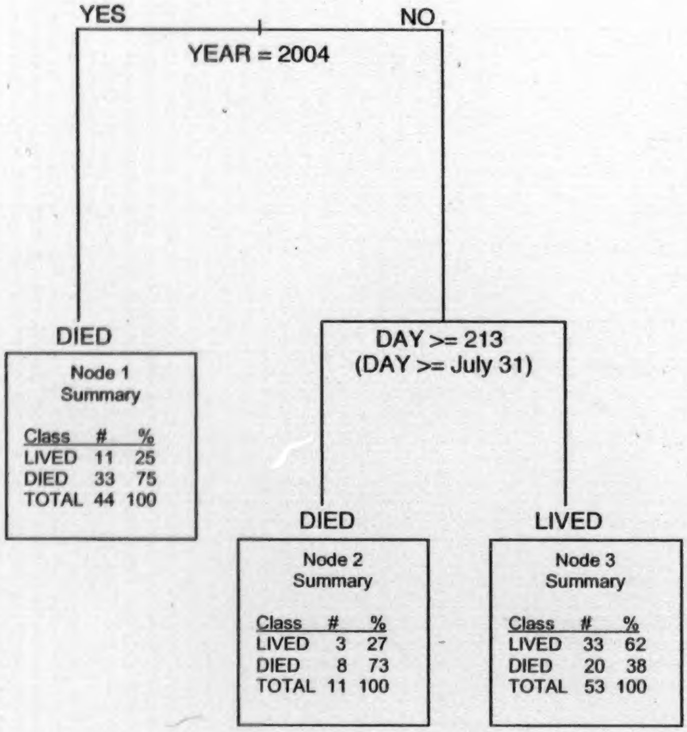
YES
NO
YEAR = 2004
DIED
Node 1
Summary
Class # %
LIVED 11 25
DIED 33 75
TOTAL 44 100
DAY >= 213
(DAY >= July 31)
DIED
Node 2
Summary
Class # %
LIVED 3 27
DIED 8 73
TOTAL 11 100
LIVED
Node 3
Summary
Class # %
LIVED 33 62
DIED 20 38
TOTAL 53 100

Figure 5-3: Classification tree to predict pika survival based on age, sex, and when haypile accumulation began, measured as day of year. Vertical line length is proportional to the amount of deviance explained by the preceding node. We report summaries for each leaf including the number and percentage of living and dead pikas.

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CHAPTER 6: DEMOGRAPHIC ANALYSIS OF A DECLINING PIKA (*OCHOTONA COLLARIS*) POPULATION: LINKING SURVIVAL TO BROAD-SCALE CLIMATE PATTERNS VIA SPRING SNOWMELT PATTERNS

Introduction

A central objective of population ecology is to determine the mechanisms underlying variation in population growth rates (e.g., the finite rate of population growth, λ) through time and across space (Krebs 2001, Turchin 2003). This variation is due to internal and external drivers that manifest their influence through vital rates such as survival and reproduction (Dobson and Oli 2001, Reid et al. 2004). Identifying the vital rates most responsible for variance in population growth is an essential initial step towards understanding the mechanistic basis of changes in population size (Tuljapurkar and Caswell 1997, Dobson and Oli 2001, Reid et al. 2004, Morris and Doak 2005), provides insights into fundamental processes in ecology and evolution, and improves our ability to predict future population abundance (Horvitz and Schemske 1995, Sibly et al. 2003a).

Vital rates differ in their relative importance to population growth and dynamics for mammals (Heppell et al. 2000, Oli and Dobson 2003), and their relative importance is a function of generation time (Charlesworth 1994, Gaillard et al. 2005) and the ratio of fertility to age at maturation (Oli and Dobson 2003). Less well understood are the differences between different populations of the same species living in a variety of environmental conditions (Coulson et al. 2005). Recent analyses have shown that vital rates differ in their relative importance to growth rate across populations of the same species. For instance, intra-specific spatial variation has been demonstrated for bighorn sheep (*Ovis canadensis*) in Alberta (Coulson *et al.* 2005), yellow-bellied marmots (*Marmota flaviventris*) in Colorado (Oli and Armitage 2004), Columbian ground squirrels (*Spermophilus columbianus*) in Alberta (Dobson and Oli 2001), and Uinta ground squirrels (*S. armatus*) in Utah (Oli et al. 2001).

Once the relative importance of multiple vital rates has been established, the next step in understanding population dynamics is to identify the ecological mechanisms underlying their variation (Coulson *et al.* 2005). For example, recent research has identified global-scale climate indices as having strong influences on wildlife populations (e.g., Post et al. 1997, Post and Stenseth 1999, Stenseth et al. 2003a) and better predictive power than local weather variables because they incorporate multiple weather components (e.g., precipitation and temperature) across appropriate temporal and spatial scales and thus capture the complex relationships between weather and ecological processes (Hallett et al. 2004, Stenseth and Mysterud 2005). Additionally, the population growth rate of different populations of the same species may be concurrently affected by both density-dependant (e.g., a functional relationship between the rate of population change and population density; Turchin 2003) and independent (e.g., climate) forces to shape observed population dynamics (e.g., Karels and Boonstra 2000, Coulson et al. 2005).

We analyzed a 12-year (1995 to 2006) census dataset from a southwest Yukon population of collared pikas (*Ochotona collaris*), a small (~140 -160 g) alpine lagomorph. Pika abundance at our site has declined dramatically since 1995, similar to reports of other Ochotonid species in North America and Asia (McDonald and Brown 1992, Beever et al. 2003, Smith et al. 2004, Li and Smith 2005). While motivated by theoretical considerations regarding mammalian life history implications on population dynamics, our analysis may also assist in determining the vital rates contributing to pika declines.

Our primary objectives were to: 1) estimate the survival and fertility rates of collared pikas within three subpopulations, 2) quantify the influence of survival and fertility rates on population growth rate using elasticity analysis and life table response experiments (LTREs), 3) determine if these patterns varied across relatively short spatial scales, and 4) test the hypothesis that pika vital rates, and therefore λ, were affected by climate influences as suggested by Beever et al. (2003) and Li and Smith (2005).

Methods

STUDY AREA

The study was conducted in a 4-km^2 alpine valley within the Ruby Range, east of Kluane Lake, Yukon, Canada (61°13' N, 138°16' W; 1600-2200 a.s.l). The valley was a mosaic of meadow and tundra vegetation interspersed with patches of talus (pika habitat; also referred to as boulderfields). Vegetation communities were dominated by *Dryas octopetala*, *Salix* spp. *Cassiope tetragona* and several graminoids (*e.g., Carex consimilis*) (Hik et al. 2001, McIntire and Hik 2005). Collared pikas, hoary marmots (*Marmota caligata*) and Arctic ground squirrels (*Spermophilus parryii*) were the dominant mammalian herbivores.

The valley had three dominant aspects (facing west, east, and south) separated by a matrix of gravel slopes, 1-2 m wide streams, and 100-300 m stretches of meadow that were unsuitable for pika colonization or persistence. The south and west aspects were connected at higher elevations by non-habitat gravel slopes that were unoccupied by pikas. The east aspect had patches of talus at higher elevations, but beyond the boundaries of our study area. The east and west aspects also were connected to talus patches outside of the valley. Census data were collected from 1995 to 2006 for the east and west subpopulations and from 1998 to 2006 for the south subpopulation.

CAPTURE METHODOLOGY

Pikas were uniquely marked and retrapped each summer from mid-June to mid-August using Tomahawk live-traps baited with fresh native vegetation. The entire study was monitored 4-5 times weekly to detect unmarked individuals that were then targeted for trapping. Pikas are diurnally active within their small (<25m radius) individual territories, have distinctive territorial calls, create easily noticed haypiles of cached vegetation (Smith 1974, 1980), permitting observers to readily locate and capture all pikas resident within the study area. These characteristics, combined with intensive trapping and search effort indicate >95% of all individuals were captured annually. Individuals trapped for the first time were marked with numbered metal ear tags (Monel #1) and a unique color combination of thin wire to allow for later re-identification from a distance. Gender was determined following Duke (1951), and individuals were classified as juveniles (young of the year) or adults (>1 year old) based on body mass and molt pattern (Franken and Hik 2004b).

Juveniles are most trappable following dispersal when they have acquired a territory and are food-hoarding (D. S. Hik, unpublished data). Because juveniles disperse from their natal territories within several days of emergence, we believe that most of our initial captures of juveniles occurred following dispersal from their natal territory. Adults at our site are philopatric and rarely switch territories (Franken 2002). We calculated population abundance as the sum of all marked individuals of all ages and sexes enumerated each season.

SURVIVAL ESTIMATION (P_A AND P_J)

Female pikas were classified as dead if not recaptured or resighted in a subsequent year. This assumption was reasonable because pikas are highly visible (Smith 1974, 1980) and adults are highly philopatric (Smith and Ivins 1983). Our long-term trapping data from an intensive trapping protocol indicated only 0.43% (n = 2 of 467) of pikas (ages and sexes pooled) were missed in any given year (i.e., marked in year t, not detected in year t+1, but re-trapped in year t+2). Thus, because the probability of recapturing all living pikas was approximately one, we did not have to account for overlooked individuals. Survival of juveniles (P_J) and adults (P_A) was calculated following Caswell (2001) for post-breeding pulse breeders.

Estimating pre-dispersal survival of young was not feasible as young are born beneath the talus and cannot be captured until emergence 30 days post-parturition (Franken and Hik 2004b). Because juvenile pikas are most easily captured once they have dispersed and established a territory, our estimates of P_J are based on female juveniles captured after dispersal.

FERTILITY (F_A)

The date of parturition at our site varied annually, but typically occurred in mid- to late-June, and does not affect over-winter juvenile survival (Franken and Hik 2004b, 2004a). Juvenile females do not reproduce in their first summer. Because pikas nests are inaccessible under the talus and juveniles disperse from the natal territory quickly following emergence to the talus surface we could not estimate mean litter size for specific females (i.e., m_A). Therefore, we calculated fecundity as the number of post-dispersal female juveniles ($N_{daughters}$) per adult female (N_{adfem}) and denote it as m_A^*. All adult females were assumed to be breeders based on data from the closely related *O. princeps* indicating >97% of adult females attempted to breed annually (Millar 1974). The sex ratio of post-dispersal juveniles was 1:1, there was no evidence of multiple litters at our site, and inter-patch dispersal behaviour of juveniles was not sex-biased (Franken 2002), so we calculated the number of daughters as 0.5 times the total number of juveniles in the population. Our estimate of fecundity, m_A^*, therefore includes juveniles born within the study area and those that dispersed into the study area. Fertility (F_A) was calculated as the product of m_A^* and adult survival (P_A) as appropriate for post-breeding designs (Caswell 2001).

$$m_A^* = \frac{0.5 \bullet N_{juveniles,i}}{N_{adfem,i}}$$

$$F_A = m_A^* P_A$$

INTER-ASPECT MOVEMENTS

The three dominant aspects of our study area (west, east, and south) appear to represent distinct pika subpopulations and are separated by 1-2m wide creeks and 100-300m of alpine meadow. Juvenile pikas at our site typically disperse within their natal talus patch (Franken and Hik 2004a). Since 1995, only 1 female moved from the subpopulation on which it was originally trapped to either one of the other two subpopulations, suggesting that movements of females is relatively uncommon. Actual inter-aspect movements may be more common than our trapping data suggests because capture of dispersing individuals (i.e., juveniles) is difficult before territory establishment.

MODEL STRUCTURE AND ANALYSIS

We parameterized female-only transition matrices according to a birth-pulse post-breeding census design (Figure 6-1; Caswell 2001), and analyzed the dataset in two ways: 1) the valley as a single population (one matrix per year from 1998 to 2006), and 2) stratified by subpopulation in which each was analyzed independently (i.e., within-subpopulation analysis). We limited our analysis in 2) to the years 1995 to 2006 for the east- and west-facing subpopulations and 1998 to 2006 for the south-facing subpopulation (Figure 6-2). In each case, we explored how projected λ responded to changes in vital rates using prospective and retrospective perturbation analysis (Caswell 2000, 2001) using MATLAB (The Mathworks, version 7.0.1 for Macintosh). Calculation of λ for a 2×2 population projection matrix is described in Appendix C.

PROSPECTIVE ANALYSIS

We examined how changes in P_J, P_A, and F_A would be reflected in λ using sensitivity and elasticity analysis on mean matrices. Other studies indicate that, in some species, λ is sensitive to the age at first reproduction (α) and last reproduction (ω) (Oli and Dobson 2003). We did not consider these in our analysis because pikas are reproductively mature at one year with no evidence of variation in α or ω (Millar 1973, 1974, Franken 2002). Sensitivity refers to the change in λ resulting from a change in matrix elements and our calculations followed Caswell (2001), where the sensitivity (s_{ij}) of λ to a change in matrix element a_{ij} is given by

$$s_{ij} = \frac{\partial \lambda}{\partial a_{ij}}$$

The elasticity (e_{ij}) of λ to a_{ij} refers to the proportional response of λ to a proportional change in a matrix element (Caswell 2000, 2001), and often are referred to as proportional sensitivities.

$$e_{ij} = \frac{\partial \log \lambda}{\partial \log a_{ij}} = \frac{a_{ij}}{\lambda} \frac{\partial \lambda}{\partial a_{ij}}$$

Although sensitivity analyses quantify how changes in vital rates (a_{ij}'s) would influence λ, they do not consider the actual changes in λ observed as a function of historical changes in vital rates (Caswell 2000).

LIFE TABLE RESPONSE EXPERIMENT (LTRE)

A LTRE is a retrospective analysis that determines how much the variances and covariances in matrix elements (i.e., P_J, P_A, and F_A) have contributed to the variance observed in λ (Caswell 2000, 2001). LTRE requires a set of matrices that represent responses to various treatments (fixed effects), or matrices from different locations or times (random design) (Caswell 2000, 2001). Given a set of matrices, it is possible to determine how variation in P_J, P_A, and F_A have contributed to V(λ) (Caswell 2000). The contribution of each element to V(λ) was calculated according to Horvitz and Schemske (1995):

$$V(\lambda) \approx \sum_{i,j} \sum_{k,l} \operatorname{cov}(a_{ij}, a_{kl}) \frac{\partial \lambda}{\partial a_{ij}} \frac{\partial \lambda}{\partial a_{kl}}$$

where cov(a_{ij},a_{kl}) is the covariance of a_{ij} and a_{kl}, and the sensitivities are calculated for the mean matrix. We used a random design because our matrices were a random sample from a distribution of possible matrices based on different subpopulations and years (Caswell 2001). Our results, therefore, reflect the contributions of variances and covariances of the matrix elements to V(λ). Eight years of census data allowed us to conduct a LTRE analysis using annual matrices for each subpopulation. Although the subpopulations were small, they were fully enumerated and represent the entire subpopulation. Therefore, parameter estimation problems associated with small sample sizes were avoided because there is no variance associated with estimates. We did not construct matrices for several census years because of missing age classes.

CLIMATE DATA

The Pacific Decadal Oscillation (PDO) is a repeating 20 - 30 year pattern of climate anomalies in sea surface temperature (SST) across the northern Pacific Ocean (Hare 1996, Mantua et al. 1997). Positive PDO values (warm phase) reflect anomalously cool SSTs in the central Pacific and warm SST along the North American coast. This is closely related to winter weather patterns throughout northwestern North America (Mantua et al. 1997, Papineau 2001) such that warm phase PDOs result in above-average winter temperatures and below average winter precipitation and snow pack conditions. The ecological and hydrogeological influence of the PDO is strong enough to be useful at forecasting forest fire activity throughout Alaska (Duffy *et al.* 2005), and has been implicated in the population dynamics of several taxa in the Pacific northwest, including salmon (Mantua et al. 1997, Schindler et al. 2005), Dall sheep (*Ovis dalli*) (Hik and Carey 2000), seabirds (Parrish and Zador 2003) and songbirds (Ballard *et al.* 2003). We correlated vital rates to winter PDO values[1] (defined here as the mean value from November to May) for each study year. We chose this period because of high rates of over-winter mortality during the winter in pikas (Franken 2002). To link the large-scale PDO to local effects we correlated winter PDO values to the timing of snowmelt on 10 permanent plots located at the centre of our study site. The permanent plots are part of a long-term study of vegetation ecology and the date each of these plots became snowfree has been documented since 1995 using dataloggers and field observations.

Results

POPULATION TRENDS

Pika population abundance (using all ages and both sexes) declined on the east and west subpopulations between 1995 and 2006 (Figure 6-2). Densities in the east subpopulation declined from 1.9 pikas/ha in 1995 to a low of

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[1] Source: http://www.cdc.noaa.gov/ClimateIndices/Analysis/

0.28 pikas/ha in 2003 before recovering to 1.4 pikas/ha in 2006. The subpopulation went locally extinct in 2000 but was recolonized the same year. Similarly, the west subpopulation declined from 2.5 pikas/ha in 1995 to a low of 0.13 pikas/ha in 2003 before recovering to 1.3 pikas/ha in 2006. This site went locally extinct during winter 2003-04 but was recolonized by July 2004 by immigrating juveniles. The south subpopulation had consistently higher population densities, greater inter-year variation, and never went locally extinct (1998-2006; Figure 6-2).

Vital Rates

We used a two-way analysis of variance (ANOVA) to determine the effects of aspect (east, west, or south), and age (juvenile or adult) on the survival rates of females. There was no evidence of an age-subpopulation interaction on survival ($F_{2,49} = 0.50$, $P = 0.61$) which allowed us to consider the main effects independently. There was no main effect of age ($F_{1,49} = 0.28$, $P = 0.60$), or subpopulation ($F_{2,49} = 1.06$, $P = 0.35$). The ratio of juveniles to female adults (m_A^*, 3.3 ± 0.81 s.e. for pooled sites, 1998-2006) did not differ by subpopulation (one-way ANOVA, $F_{2,22} = 0.09$, $P = 0.91$), nor did female fertility (F_A, $F_{2,22} = 0.51$, $P = 0.61$).

Correlation of Climate and Population Abundance with Vital Rates

When the entire study site was analyzed as a single population (i.e., pooled subpopulations), adult female survival (P_A) was positively correlated to the mean winter PDO with a time lag of one year (Pearson's $r = +0.77$, $P = 0.03$, Figure 6-3A). Adult survival was uncorrelated to the PDO in the absence of a lag ($r = -0.01$, $P = 0.99$), or population density ($r = -0.19$, $P = 0.65$). Adult fertility (F_A), and the number of juveniles per adult female (m_A^*), were negatively correlated to the number of adult pikas ($r = -0.68$, $P = 0.06$ and $r = -0.62$, $P = 0.10$, respectively). Juvenile survival (P_J) was not correlated to either the PDO ($r = 0.571$, $P = 0.140$) or the number of adult pikas ($r = 0.02$, $P = 0.955$).

Adult survival and juvenile survival were positively correlated to the lagged winter PDO on the south-facing subpopulation (r = +0.80, $P = 0.017$, and r = +0.77, $P = 0.03$, respectively, Figure 6-3B). On the east-facing subpopulation, juvenile survival was positively correlated with the lagged PDO (r = +0.65, $P = 0.03$), while m_A^* was negatively correlated to adult density (r = -0.64, $P = 0.06$). On the west-facing subpopulation, P_A and m_A^* were correlated to adult density (r = +0.63, $P = 0.10$ and r = -0.70, $P = 0.06$, respectively). No other vital rates were correlated (i.e., $P < 0.10$) to the PDO or adult density for any subpopulation.

The winter PDO values were strongly correlated to the timing of snowmelt at the permanent plots located at the centre of our study site (r = -0.87, Figure 6-4). Negative PDO values were associated with later snowmelt whereas positive PDO values were associated with an earlier disappearance of snow from the plots.

PROSPECTIVE ANALYSIS

Population growth rate was most sensitive to changes in P_J and P_A when the population was considered as a single population. Growth rate was approximately equally elastic to P_A, P_J, and F_A for the pooled population (Table 6-1). The rank order of sensitivities varied by subpopulation when considered separately: λ was most sensitive to P_A and P_J in the east- and south-facing subpopulations, but to P_A and F_A in the west-facing subpopulation. Elasticities also varied by subpopulation but the trends were less clear. Growth rates on the east- and south-facing subpopulations were approximately equally sensitive to each non-zero matrix element, whereas λ was more elastic to P_A on the west-facing subpopulation.

RETROSPECTIVE ANALYSIS

LTRE analysis of the pooled study site suggested that the matrix element(s) that had made the largest contribution to $V(\lambda)$ were those based on adult vital rates (P_A and F_A); variation in these combined rates explained 79.1% of $V(\lambda)$ (Table 6-1). This pattern was similar when each subpopulation was analyzed separately. Variation in P_J contributed only 18.2 to 20.7% to $V(\lambda)$ for any subpopulation. Instead, matrix elements based on the vital rates of adults contributed most to $V(\lambda)$. Adult fertility (F_A) contributed most to $V(\lambda)$ in the east- and south-facing subpopulations (48.9 and 48.8%, respectively), whereas P_A contributed most (495) to $V(\lambda)$ for the west-facing subpopulation. Overall, adults contributed 79.3 to 81.7% (P_A plus F_A) to $V(\lambda)$ in each subpopulation (Table 6-1).

Discussion

Population dynamics are determined by the underlying vital rates of the population that, in turn, are determined by a number of factors including environmental conditions, density dependence, and chance events, among others. The demographic basis underlying changes in λ is a fundamental issue in population ecology (Sibly et al. 2003b), yet it remains poorly understood for many vertebrate populations (Dobson 1995). In this light, the results of our study provide several main conclusions. First, we demonstrated a sequence of strong relationships between large-scale climate patterns (PDO), the timing of snowmelt in spring, adult survival rates, and ultimately, variation in pika population growth rates. Second, the vital rates of some pika subpopulations were concurrently affected by density-independent factors like climate (e.g., adult survival, P_A) while others (e.g., fecundity, m_A^*) were most affected by density. Reduced reproduction through loss of entire litters at high population densities also has been observed in *O. princeps* (Millar 1974). Our observation of density-dependant (i.e., fecundity) and density-independent (i.e., survival) factors operating simultaneously adds to a small, but growing, body of research that suggests both factors often combine to shape population dynamics (e.g., Karels and Boonstra 2000, Stenseth et al. 2003b). Third, the vital rates of nearby subpopulations may show little or no detectable relationships with either climate patterns or density, suggesting the influence of other local factors.

There is accumulating evidence that the vital rates most responsible for variation in population growth vary among populations of the same species. For example, experimental manipulation of food resources indicated that population declines of Columbian ground squirrels were driven by juvenile survival in some, but not all, of the populations (Dobson 1995). Mortality of bighorn sheep in Alberta explained 44% of variance in growth rate in one population, but only 15.3% in another population (Coulson *et al.* 2005). At our site, adults were responsible for most of the variation in growth rate, whether through survival or fertility. Their relative importance, however, varied spatially at distances <300m between subpopulations.

Because fitness is measured by λ, determining those life history traits that most affect λ will also identify the intensity of natural selection on those traits (Benton and Grant 1996, Pfister 1998, Caswell 2001). Spatiotemporal variation in the trait most affecting λ implies that the corresponding fitness response is also spatiotemporally variable (Horvitz and Schemske 1995). Therefore, at our site, the intensity of selection on a given vital rate may also differ by subpopulation. North American pika populations (*O. princeps* and *O. collaris*) have been variously described as stable (Millar 1973, Smith et al. 2004) or variable (Smith 1978, Franken 2002). Fluctuations in population abundance are likely due to environmental variation, such that pikas in regions of high environmental variation tend to have greater variability in population abundance (Smith 1978).

Pikas at our site have declined and then increased again in two subpopulations (east and west), but have been variable in the south subpopulation with no clear trend. Variation in winter weather patterns appears to be the most plausible explanation for declining populations at our site. Adult survival was strongly correlated to high PDO values that tend to reflect below average snow-pack conditions (Mantua et al. 1997, Papineau 2001). The effects of the PDO on local conditions at our site are exerted through the timing of snow-pack melt in spring. Earlier snowmelt should result in earlier growth of high-quality vegetation and, subsequently, improved body condition of pikas during the spring breeding season and remainder of the summer. Further, an earlier snowmelt may produce a longer growing season for vegetation allowing pikas additional time to collect vegetation for their haypiles.

Field observations show that snowmelt is not uniform across the site and this may partially explain differences between aspects. For example, snow melt seemed to occur earlier on south aspects at our site (D. S. Hik, unpublished data) and may explain why that site has not experienced the same population decline as the east or west subpopulations in a manner similar to that reported by Kreuzer and Huntly (2003). We did not observe a correlation between climate (i.e., PDO) and reproduction, although this relationship has been reported for *O. princeps* (Smith (1988), but see Millar (1974)). Variation in spring snow melt has also been implicated in the population dynamics of other alpine species such as reindeer (*Rangifer tarandus*; Pettorelli *et al.* 2005) and hoary marmots (Marmota caligata; Karels and Hik 2003).

Weather may also be implicated in collared pika declines through catastrophic winter mortality associated with rain that later freezes forming an icy crust over food resources rendering them unavailable; alternatively winter rain may directly cause pika death through exposure (Smith *et al.* 2004). The frequency of winter freezing and thawing events in alpine and high latitude ecosystems is predicted to increase as a consequence of global warming (IPCC 2001, ACIA 2005). Increasing amounts of winter precipitation falling as rain rather than snow, attributed to the PDO and climate change trends, has recently been documented in western United States (Knowles et al. 2006), leading to an expectation of more frequent freeze-thaw events in the future. Such freeze-thaw events have been implicated in the population dynamics of other high-latitude herbivores (e.g., Forchhammer and Boertmann 1993, Aanes et al. 2000, Aars and Ims 2002). Alternatively, the trend of earlier snowmelt, also documented by Knowles et al. (2006), could improve pika survival and positively affect pika populations. The relationships we observed between vital rates and the PDO provide support in favor of the hypothesis linking pika population growth to winter weather conditions and warrant further detailed investigation.

CONCLUSION

The decomposition of V(λ) into contributions from matrix elements is a powerful tool in understanding how λ responded to historical environmental variation, and can substantially contribute to our understanding of population dynamics. Population declines and fluctuations at our site were driven largely by variation in adult vital rates, however, the specific influence of adults varied spatially. The variation in adult survival was well explained by large-scale climate patterns (the Pacific Decadal Oscillation) and demonstrated a strong link between large-scale climate indices and population growth rate through the timing of spring snowmelt and intermediary vital rates.

Table 6-1: Results of sensitivity, elasticity, and LTRE analysis of three subpopulations of collared pikas in southwestern Yukon. It is the property of age-structured matrices that the sum of any row in an elasticity matrix equals the sum of the corresponding column (De Kroon et al. 1986, Heppell et al. 2000). Therefore, the elasticities of λ to F_A and P_J will necessarily be equal given projection matrix **A**. The LTRE contribution refers to the percentage of variance in the projected population growth rate, V(λ), explained by each vital rate.

Subpopulation & Vital rate	Sensitivity	Elasticity	LTRE contribution (%)
Entire valley (subpopulations pooled)			
P_J	0.628	0.321	20.9
F_A	0.347	0.321	43.5
P_A	0.679	0.357	35.6
East-facing			
P_J	0.786	0.304	20.7
F_A	0.269	0.304	48.9
P_A	0.696	0.393	30.4
West-facing			
P_J	0.425	0.267	18.2
F_A	0.460	0.267	32.2
P_A	0.733	0.466	49.5
South-facing			
P_J	0.496	0.306	20.1
F_A	0.428	0.306	48.8
P_A	0.694	0.389	31.1

$$A = \begin{bmatrix} 0 & F_A \\ P_J & P_A \end{bmatrix}$$

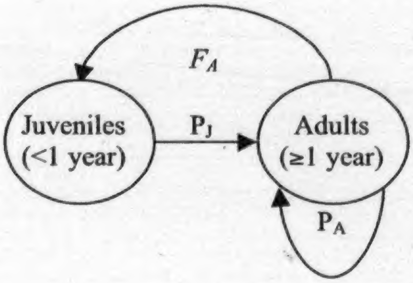

Figure 6-1: Projection matrix and life cycle for female collared pikas in southwestern Yukon. Matrices were parameterized according to a post-breeding census. Collared pikas do not breed in their first summer and are reproductively mature adults after their first winter. P_J = juvenile female survival, P_A = adult female survival, F_A = fertility of adult females

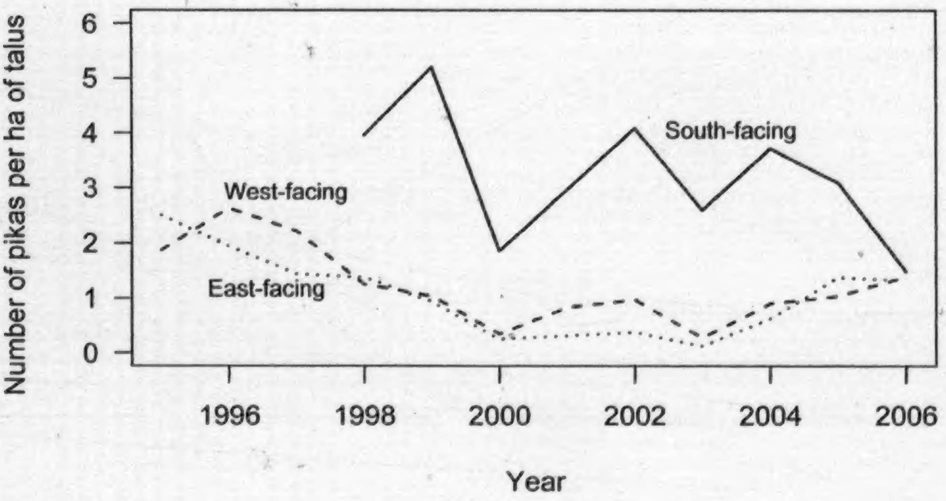

Figure 6-2: August density of three subpopulations of collared pikas, 1995-2006, in southwestern Yukon. Values represent the total number of territorial pikas of all ages and both sexes per hectare of talus habitat. Abundances were derived from a complete enumeration of live-trapped individuals with uniquely colored eartags.

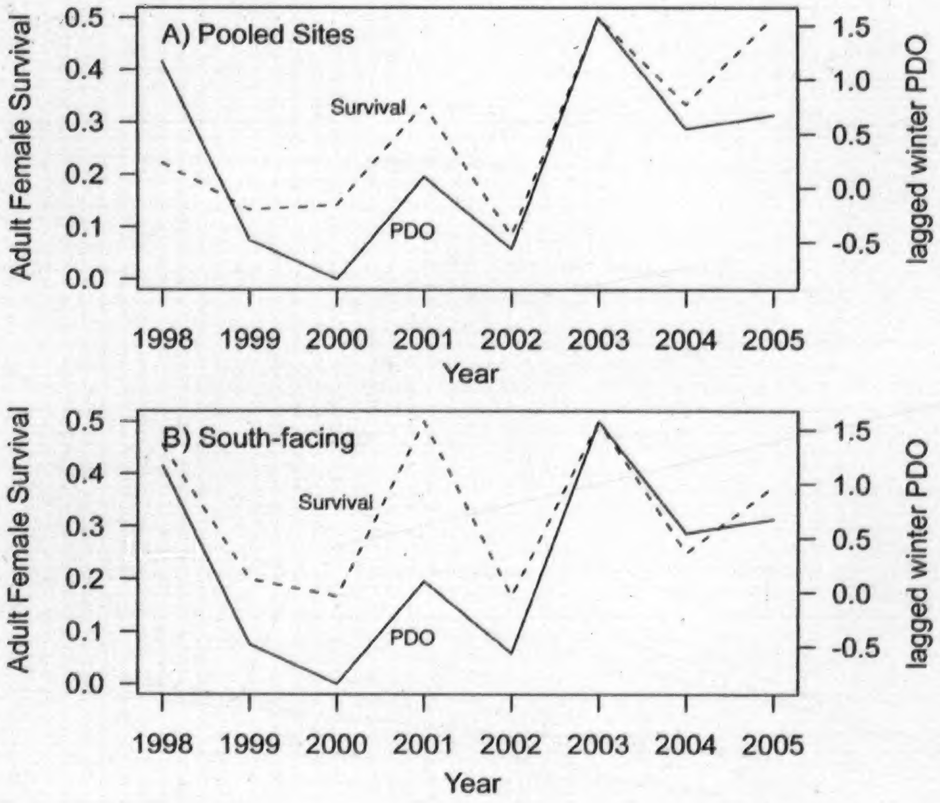

Figure 6-3: Relationship between adult female survival in year *t* and the winter Pacific Decadal Oscillation for winter *t*-1 for A) the entire study site (i.e., pooled subpopulations) and B) the south-facing subpopulation.

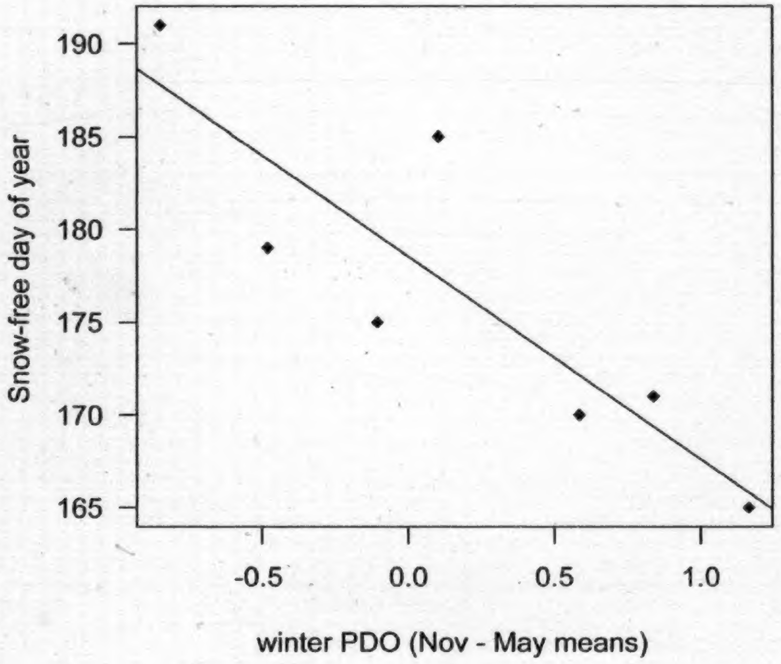

Figure 6-4: Relationship between the winter Pacific Decadal Oscillation (mean Nov – May) and snow-free date between 1995 and 2001. Snow-free date was the day of year in which permanent plots were free of snow as determined by data-loggers and field records.

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CHAPTER 7: FURTHER EVIDENCE THAT OCHOTONIDS ARE AT RISK OF EXTINCTION: A PVA FOR COLLARED PIKAS

Introduction

Alpine ecosystems, particularly those at high latitudes, are projected to be one of the first types of ecosystems negatively affected by global climate warming (ACIA 2005). Detection and monitoring the extent and rate of ecosystem change will increasingly require the use of climate-sensitive species. Candidate taxa would be climate-sensitive with large geographic ranges to improve the robustness and generality of observed patterns. Rock-dwelling members of the Ochotonidae may be particularly useful as climate change indicators because of their extreme sensitivity to increased temperatures (Smith 1974b, McDonald and Brown 1992, Grayson 2005) and strikingly similar morphology, behaviour and life history (Smith et al. 1990).

Populations of rock-dwelling pikas appear to be declining worldwide (Smith et al. 2004). The Ili pika (*O. iliensis*) was discovered in the Tian Shan Mountains, China in 1983 (Li and Ma 1986). However, by 2003, extensive searches of all known populations indicated that only 43% (n = 6 of 14) of populations were still extant, indicating a rapid decline toward extinction (Li and Smith 2005). Similarly, the American pika (*O. princeps*) has been extirpated at 28% (n = 7 of 25) of historically sampled populations in the Great Basin region of North America within the past century (Beever et al. 2003). Detailed census records for the collared pika (*O. collaris*), endemic to Yukon and Alaska, indicate population decline between 1995 and 2006 (Figure 6-2). Global climate change is the most cited hypothesis to explain recent declines for both species (McDonald and Brown 1992, Beever et al. 2003, Li and Smith 2005). Paleontological data supports this hypothesis and demonstrates that *O. princeps* has been declining in the Great Basin since the late-Wisconsonian and is in danger of extinction as the climate warms (Grayson 2005).

The collared pika (*O. collaris*) is a rock-dwelling species endemic to Yukon and Alaska. Long-term demographic and census data indicate declining population abundance since at least 1995 (Figure 6-2). To assess the future status of this population we conducted a series of demographic-based population viability analyses (PVAs). To our knowledge, this is the first PVA conducted for any rock-dwelling member of the Ochotonidae.

Material and methods

STUDY AREA

The study was conducted in a 4-km^2 alpine valley within the Ruby Range, east of Kluane Lake, Yukon, Canada (61°13' N, 138°16' W; 1600-2200 m a.s.l). The valley was a mosaic of meadow and tundra vegetation interspersed with patches of talus. Vegetation communities were dominated by *Dryas octopetala*, *Salix* spp. *Cassiope tetragona* and several graminoids (*e.g., Carex consimilis*) (Hik et al. 2001, McIntire and Hik 2005). Collared pikas, hoary marmots (*Marmota caligata*) and Arctic ground squirrels (*Spermophilus parryii*) were the dominant mammalian herbivores.

The valley had three dominant aspects facing west, east, and south, and separated by a matrix of non-habitat (gravel slopes, 1- to 2-m wide streams, and 100- to 300-m stretches of meadow). The south- and west-facing aspects were connected at higher elevations by non-habitat gravel slopes that were unoccupied by pikas. The east-facing aspect had patches of talus at higher elevations but beyond the boundaries of our study area. The east and west aspects also were connected to talus patches outside of the valley.

CAPTURE METHODS

Pikas were captured each summer using Tomahawk live-traps baited with fresh native vegetation. We were able to readily locate and capture all pikas resident within each patch because they are diurnally active within their small (<25m radius) individual territories, have distinctive territorial calls, and create easily noticed haypiles of cached vegetation (Smith 1974b, 1980). Individuals trapped for the first time were marked with numbered metal ear tags (Monel #1) and a unique color combination of thin wire to allow for later re-identification from a distance. Gender was determined following Duke (1951) and individuals were classified as juvenile or adult based on body mass and molt pattern (Franken and Hik 2004b). Juveniles were most trappable following dispersal when they have acquired a territory and are food-hoarding (D. Hik, unpublished data). Pikas dispersed from their natal territories within several days following emergence, therefore we believe that most of our initial captures of juveniles occurred following dispersal from their natal territory.

SURVIVAL ESTIMATION

Female pikas were classified as dead if not recaptured or resighted in a subsequent year. This assumption was reasonable because pikas are highly visible (Smith 1974b, 1980) and adults are highly philopatric (Smith and Ivins 1983). Our long-term census data from an intensive trapping protocol indicated only 0.43% (n = 2 of 467) of pikas were missed in any given year (i.e., marked in year t, not detected in year $t+1$, but re-trapped in year $t+2$). Thus, because the probability of recapturing all living pikas was approximately one, we did not have to account for overlooked individuals in survival estimates. Survival of juveniles (P_J) and adults (P_A) was calculated following Caswell (2001) for post-breeding pulse breeders. Estimating pre-dispersal survival of young was not feasible as young are born beneath the boulderfield (talus) and cannot be captured until emergence 30 days post-parturition (Franken and Hik 2004b). Therefore, our estimates of juvenile survival were based on juveniles captured after dispersal. Previous studies of this population indicated no gender-based differences in juvenile survival (Franken 2002), and we therefore pooled male and female juveniles to estimate P_J.

FERTILITY (F_A)

Parturition at our site varied annually, but typically occurred in mid- to late-June, and does not affect over-winter juvenile survival (Franken and Hik 2004b, 2004a). Because pika nests are inaccessible under the talus and juveniles disperse from the natal territory quickly following emergence to the talus surface we could not estimate mean litter size for specific females (i.e., m_A). Therefore, we calculated fecundity as the total number of post-dispersal female juveniles ($N_{daughters}$) per adult female (N_{adfem}). The total number of juveniles includes juveniles born within the study site and those that immigrated into the study site. Therefore, we denote our estimate of fecundity as m_A^* to reflect juvenile production. The sex ratio of pika litters was approximately 1:1, and there was no evidence of multiple litters at our site (Franken 2002), so we calculated the number of daughters in year *i* as 0.5 times the total number of juveniles in the population. Fertility (F_A) was calculated as the product of m_A^* and adult survival (P_A) as appropriate for post-breeding designs (Caswell 2001).

$$m_A^* = \frac{0.5 \bullet N_{juveniles,i}}{N_{adfem,i}}$$

$$F_A = m_A^* P_A$$

MODEL STRUCTURE & ANALYSES

We parameterized female-only population projection matrices according to a birth-pulse post-breeding census design (Caswell 2001). Our analyses used life-history data from 301 pikas (Table 7-1) that was used to parameterize a projection matrix for each year from 1998-99 to 2005-06. We considered a variety of scenarios including all data, restricting the dataset to the best sites and the years of highest adult female survival, or some intermediate set of conditions (Tables 7-1 and 7-2). The best four years of adult female survival across the entire site were 2001-02, 2003-04, 2004-05, and 2005-06. We considered the south aspect as the best site because it had consistently higher population density and did not indicate a declining trend, unlike the other two aspects (Figure 6-2).

Stochastic Log Growth Rates

We estimated the stochastic log growth rate, log(λ_s), in two ways. First, we used simulations in which the population was projected through 50 years by randomly selecting a matrix for each annual time step. The log(λ_s) was calculated as the mean of $\log(N_{t+1}/N_t)$, where N_t is the number of individuals in year t. This procedure was iterated 10,000 times to determine 95% confidence limits. Second, we estimated log(λ_s) analytically with Tuljapurkar's (1982) approximation:

$$\log \lambda_s \approx \log \overline{\lambda}_1 - \frac{1}{2}\left(\frac{\sum_{i=1}^{s}\sum_{j=1}^{s}\sum_{k=1}^{s}\sum_{l=1}^{s} Cov(a_{ij},a_{kl})\overline{S}_{ij}\overline{S}_{kl}}{\overline{\lambda}_1^2} \right),$$

where λ_1 refers to the dominant eigenvalue of the mean projection matrix, Cov(a_{ij},a_{kl}) refers to the covariation among matrix elements a_{ij} and a_{kl}, and $\overline{S}$ refers to the sensitivity of λ_1 to variation in matrix elements. Tuljapurkar's (1982) approximation assumes that the variances and covariances of the matrices vary little over time, although the technique is relatively robust to violations of this assumption (Morris and Doak 2002).

Simulations of Extinction Risk

Our simulations closely followed methods detailed by Morris and Doak (2002). We used two methods to analyze extinction risk. First, we simulated the extinction time cumulative distribution function by projecting the population over 50 years using an annual time step and assuming an 'independently and identically distributed' (*iid*) stochastic environment. For each time step a projection matrix was drawn at random from the set of available matrices. The initial population vector was the number of female juveniles and adults in 2006, and we used a quasi-extinction threshold of one individual. This process was repeated for 10 runs of 1000 individual realizations of population trajectories per run.

Results

STOCHASTIC LOG GROWTH RATE, LOG(λ_S)

Estimates of the stochastic log population growth rate, log(λ_s), indicated a declining population for scenarios A through F (Table 7-2). Simulation estimates of log(λ_s) based on simulations for scenarios A through F ranged from -0.806 to -0.043. Only scenario G had a log(λ_s) that exceeded zero ($\bar{x}$ = +0.010, 95% CI = +0.003 to +0.017), indicating an increasing population. Analytical estimates using Tuljapurkar's (1982) approximation were consistent with the simulated estimates in estimating population growth rate for all scenarios (Table 7-2, Figure 7-1).

EXTINCTION RISK

Scenarios A - E indicated a very high probability of extinction within 50 years (Figure 7-1). This result was consistent when either simulations or Tuljapurkar's (1982) method were used. The inclusion of all years of available data from throughout the entire study area (Scenario A) resulted in a >90% probability of extinction within 10 - 15 years. Restriction of the dataset to individuals from the highest quality site (south-facing aspect) and to the best four years of adult female survival (i.e., best-case scenario; Scenario E, Figure 7-1) still produced a >90% probability of extinction within 50 years from present. Extinction risk declined appreciably only when adult survival was increased by 25% above the best-case scenario (Scenario F, Figure 7-1).

Discussion

This is the first population viability analysis conducted for any rock-dwelling member of the Ochotonidae. In our analyses, we have considered seven scenarios ranging from the inclusion of the full dataset (Scenario A), to limiting our dataset to the 'best-case' scenario (Scenario D), to investigating the effects of improved adult female survival (Scenarios E-G). For many of the scenarios considered in this analysis (i.e, scenarios A-E), this collared pika population has a >90% probability of extinction within the next 50 years. Other rock-dwelling pika species and populations, many facing greater threats than collared pikas, are similarly at risk (Grayson 2005, Li and Smith 2005). Because of their characteristic central-place foraging behaviours (Huntly et al. 1986, Holmes 1991, Morrison et al. 2004), a loss of pikas from alpine ecosystems could elicit a trophic cascade of changes in soil nutrient cycling (Aho et al. 1998), plant biodiversity (Huntly 1987, McIntire and Hik 2005), and plant life-history patterns (McIntire and Hik 2002, 2005).

Rock-dwelling pikas like *O. collaris* and *O. princeps* are examples of classical metapopulations, such that they occupy highly fragmented landscapes consisting of patches of talus habitat interspersed by an inhospitable matrix of alpine meadow (Smith and Gilpin 1997, Moilanen et al. 1998). Local populations are connected only by juvenile dispersal with most other life history events occurring at an intra-patch spatial scale due to extremely high adult philopatry (Smith and Ivins 1983, Franken 2002).

Rock-dwelling pika species may have difficulty avoiding local extinctions because of limited dispersal abilities, small population sizes, and low densities (Smith 1974a, 1988, Smith et al. 1990, Franken 2002) and these local extinctions may affect regional population persistence (Smith and Gilpin 1997). Our analysis is conservative because we did not include 1) the continued influence of a rapidly warming and increasingly variable Yukon climate (Zhang et al. 2000, ACIA 2005) known to reduce pika survival through winter freeze-thaw events (Smith et al. 2004), or 2) human-related mortality such as the open-season, no bag limit, commercial trapping recently approved for *O. collaris* in Game Management Units 12 and 20E in Alaska (Alaska Board of Game, Proposal 108, carried March 2006).

Chapter 6 of this thesis suggested that population growth rate was strongly correlated to the mean November-May Pacific Decadal Oscillation (PDO), a large-scale climate pattern with a 20 - 30 year period (Hare 1996, Mantua et al. 1997, Mantua and Hare 2002). Although we have 8-years of census data, we were unable to speculate how pikas will respond to PDO events not observed during the course of this study. We do not have data to fully assess these effects on future pika survival or the persistence of this population and therefore our analyses assumed an identical and independently distributed environment.

Until adequate data are obtained, we suggest that any management action that reduces survival or fertility of collared pikas should be avoided. Rock-dwelling pikas are an established indicator species for the effects of climate warming (Smith et al. 1990, Smith et al. 2004, Grayson 2005), therefore other alpine species could be experiencing similar declines. Monitoring of other populations of pikas is warranted to determine whether our site is representative of the overall status of these species.

Table 7-1: Number of juvenile and female adult pikas from southwest Yukon used to construct population projection matrices for population viability analysis. Note that sample sizes were based on complete census data collected from 1998 to 2006.

Year	Entire Study Site		Best Site (south-facing slope)		Year Included per Scenario[1]			
	Juveniles[2]	Adult Females	Juveniles[2]	Adult Females	A	B	C	D-G
1998	24	27	9	11	√		√	√
1999	37	15	15	10	√		√	
2000	10	7	5	6	√		√	
2001	31	6	17	4	√	√	√	√
2002	25	12	15	6	√		√	
2003	10	6	4	6	√	√	√	√
2004	37	9	17	8	√	√	√	
2005	29	16	14	8	√	√	√	√
Total	203	98	96	59				

[1] Checkmarks indicate the years of data included in each of the six PVA scenarios. See Table 7-2 for descriptions of each scenario.

[2] The number of juveniles includes both sexes. See text for calculations of survival and fertilities.

Table 7-2: Seven scenarios used for extinction risk analysis. The best site was defined as the south-facing aspect and the best years represented the 4 best years of adult survival. The stochastic log lambda (log λ_s) was calculated using a) 10,000 computer simulations (presented as mean values with 95% confidence intervals in parentheses), and b) Tuljapurkar's (1982) approximation.

Scenario	Description	log λ_s	
		Simulation	Tuljapurkar
A	Entire study site, 1998-2006	-0.806 (-0.820 to -0.792)	-0.775
B	Entire study site, 4 best years	-0.246 (-0.250 to -0.242)	-0.245
C	Best site, 1998-2006	-0.673 (-0.683 to -0.662)	-0.682
D	Best site, 4 best years	-0.198 (-0.205 to -0.192)	-0.197
E	Scenario D, with adult survival increased by 10%	-0.131 (-0.138 to -0.125)	-0.130
F	Scenario D, with adult survival increased by 25%	-0.043 (-0.050 to -0.036)	-0.040
G	Scenario D, with adult survival increased by 35%	+0.010 (+0.003 to +0.017)	+0.015

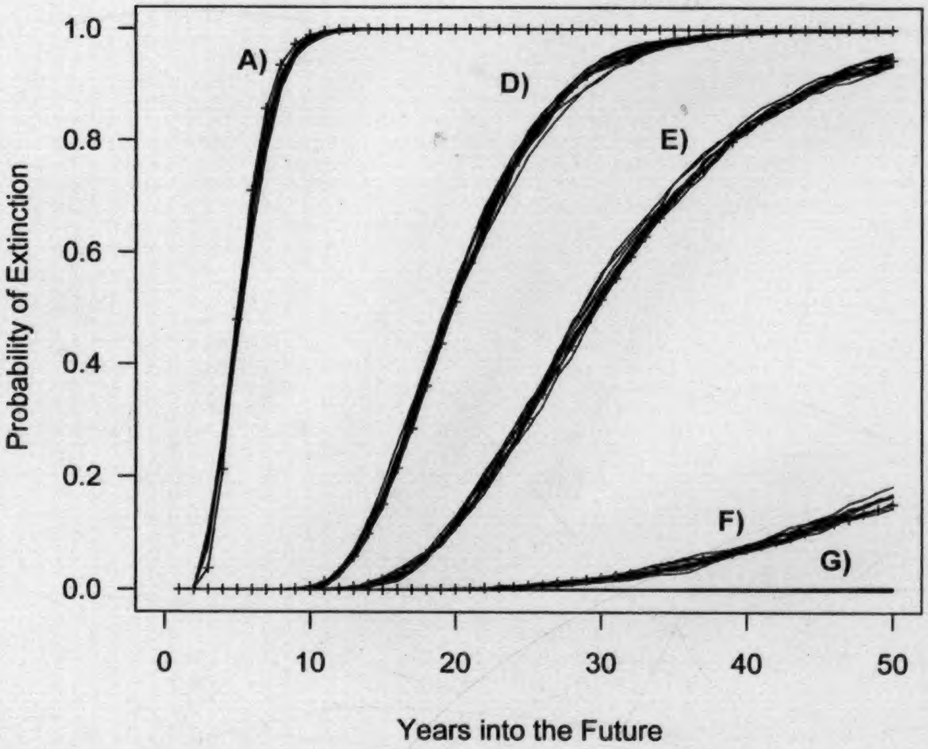

Figure 7-1: Cumulative probability of extinction for collared pikas over 50 years based on live-trapping census data from southwestern Yukon (1998-2006). Each line type represents an individual scenario: A) all available data, D) dataset restricted to the highest quality site and the four years of highest adult female survival, E-G) the effects of increasing adult female survival values in D) by 10, 25, and 35%. Scenarios B) and C) are intermediate between A) and D) and are not shown. Lines without markers are simulations, lines marked with '+' are based on Tuljapurkar's (1982) method.

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CHAPTER 8: CONCLUSIONS

Pikas, like most herbivores, constantly are confronted with multiple decisions that affect their nutritional status and life history traits. Superimposed on these decisions are the effects of seasonality and its variation in resource quality, quantity, and favorable living conditions. Strongly seasonal environments, such as the contrasting summer and winter conditions in the Ruby Range, force pikas to adapt their foraging behaviour to contend with these changes. In its simplest form, this strategy requires surviving winter until the following spring reproductive season and vegetation green-up. Foraging behaviours and decisions therefore have important effects on pika population dynamics. This thesis addressed several of these questions and improved our understanding of climate-plant-herbivore interactions in alpine environments. A conceptual diagram of the climate-plant-herbivore interactions examined in this thesis is provided in Figure 8-1.

Predation risk, forage quality, and their effects on haying decisions

Collared pikas restrict their foraging and haying efforts to a narrow band of vegetation surrounding talus (Holmes 1991, McIntire and Hik 2002, 2005), in a manner similar to the American pika (Huntly et al. 1986, Roach et al. 2001). Holmes (1991) experimentally added protective talus cover in meadows and collared pikas responded by foraging and haying at greater distances into the meadow. Therefore, foraging and haying behaviours were strongly affected by predation risk. My experimental work in **Chapter 2** added to Holmes' (1991) study on predation-sensitive foraging in several ways. First, I confirmed pikas were strongly affected by predation risk, such that they removed progressively less vegetation from the cafeterias as distance from protective talus increased. This is analogous to the concept of a 'giving up density', where foraging decisions can be measured by recording relative changes in consumption under different conditions. The addition of protective cover removed this pattern and confirmed that the response was primarily due to predation risk and not other potentially confounding factors, such as handling time.

Secondly, foraging theory predicted that central place foragers such as pikas should become increasingly selective as the cost (measured as travel time or level of predation risk) of foraging increased (Stephens and Krebs 1986, Lima and Dill 1990). Research on *O. princeps* showed that pikas were more selective, less vigilant, and traveled greater distances into the meadow when haying than when grazing (Huntly et al. 1986, Dearing 1996, Roach et al. 2001). **Chapter 2** expanded on these studies by asking how plant selection during haying varied with predation risk (rather than comparing haying and foraging). The results showed that pikas did not change their selection of individual species as predation risk increased, despite being presented with plant species that varied across a range of nutritional quality. These results improved our understanding of how pikas modify the structure of vegetation communities (e.g., Roach et al. 2001), because although foraging intensity decreased with distance from talus, the effect of haying pikas remained constant in terms of species selection. In other words, their selection criteria were not contingent on predation risk. Plant-herbivore models (e.g., Owen-Smith 2002) for pikas can assume that forage preferences are consistent within the band of vegetation surrounding talus patches.

A herbivore's nutritional environment is more complex than simply ranking available forage species. A mechanistic understanding of forage selection should consider the specific nutritional characteristics by which herbivores evaluate their foraging options (Robbins 1983). Previous studies on *O. collaris* and the closely related *O. princeps* indicated that plant selection was based on nutritional characteristics such as protein and water content (Millar and Zwickel 1972, Smith 1974, Holmes 1991, Dearing 1996). To test these ideas, we experimentally manipulated the protein and water content of two common forage species, *Carex consimilis* and *Polygonum bistorta*, and measured their influence on inter- and intra-specific selection (**Chapter 3**). Manipulation of forage quality revealed complex interactions between water content and crude protein levels for individual species, and indicated pikas make both inter- and intra-specific decisions. Therefore, the forage selection decisions made by pikas during haying were more specific than previously known.

The observed and predicted climate warming at high-latitudes (Zhang et al. 2000, ACIA 2005) has the potential to increase nutrient cycling and affect plant biomass, nutritional quality, and species diversity (Starr et al. 2000, Jónsdóttir et al. 2005). Experimental warming of *Carex bigelowii* (a species complex of which *C. consimilis* is a member) caused a reduction in forage quality without a compensatory increase in above-ground biomass (Jónsdóttir et al. 2005). In another study, *Polygonum bistorta* did not respond to experimentally lengthened growing seasons, indicating it was less able to compete against more plastic species given projected changes in growing season length (Starr et al. 2000). Pikas detected subtle inter- and intra-specific variation in forage quality indicators such as crude protein levels (**Chapter 3**), therefore it follows that forage selection by pikas may be altered by changes in the vegetation community due to climate warming. The effects of those changes on pikas are currently unknown. In turn, changes in plant selection may have important feedback effects on plant communities along the talus margin by altering nutrient cycling or competitive interactions (Mitchell 2006).

Linking caching behaviour to populations dynamics

Animals cache food to control its availability and quality during times of food scarcity, allowing them to partially escape the adverse consequences of scarcity (Vander Wall 1990). The caching behaviour of pikas has been well documented (Broadbooks 1965, Krear 1965, Millar and Zwickel 1972, Barash 1973, Conner 1983). However, the relationship between haying behaviour and population-level consequences remains uncertain (Millar and Zwickel 1972, Conner 1983, Dearing 1997).

Two chapters in this thesis addressed the link between pika haying behaviour and population-level responses. First, we estimated haypile mass and the number of days of food contained within a typical haypile (**Chapter 4**). Measurement and simulation of haypile mass indicated that pikas stored enough vegetation to serve as the sole source of food for > 5.9 months, supporting Dearing's (1997) argument that haypiles serve as more than a 'bet-hedging' strategy to survive abnormally long winters (Millar and Zwickel 1972, Conner 1983). Pikas made an enormous effort (>11600 trips each summer) to accumulate haypile vegetation (**Chapter 4**). Such a large effort repeatedly exposed individuals to predation risk during summer. Therefore, the over-winter survival benefits gained by haying should exceed the immediate risk of being killed by a predator during summer.

Chapter 5 further addressed the link between pika haying behaviour and population dynamics by documenting the annual onset of haying behaviour for known individuals and relating this to their subsequent over-winter survival. The annual onset of haying activity had an important, but inconsistent, effect on pika over-winter survival. Earlier onset of haying had no effect on survival during the 2004-05 winter, but positively affected survival during the 2005-06 winter and suggested multiple sources for variation in over-winter survival, some of which over-rode the importance of haying behaviour (e.g., annual variation in winter predation or freeze-thaw events). The combined results of **Chapters 4 and 5** indicated a strong link between pika foraging behaviour and population dynamics through its effect on over-winter survival.

Full circle: Population dynamics, climate, and spring vegetation growth

A population's rate of growth (λ) is driven by mechanisms such as density-dependence or climate patterns that exert their influence on the population through vital rates such as fecundity or survival (Caswell 2001, Sibly et al. 2003). Recent work showed that the intra-specific demographic drivers of λ can vary across relatively short distances (e.g., Oli and Armitage 2004, Coulson et al. 2005). We used long-term census data to estimate the contribution of fertility and survival to variance in pika population growth and searched for the mechanistic basis of changes in population size (**Chapter 6**). Life-table response experiments (LTREs) indicated the population decline observed at our site was driven largely by variation in adult survival and adult fecundity. Juveniles had very little influence. This pattern was consistent whether the entire study site was analyzed as a single unit, or analyzed separately for each of the three subpopulations.

Female adult survival in the south-facing subpopulation was strongly correlated to the Pacific Decadal Oscillation (PDO) with a time lag of one year implicating the importance of earlier spring conditions and plant phenology on the subsequent winter survival of adults and therefore population growth (**Chapter 6**). However, adult survival and fertility were not significantly correlated to the PDO, or the timing of spring snowmelt, in either the east or west subpopulations. This indicated that the mechanisms underlying variation in population growth rate can vary substantially over relatively short distances.

The snowmelt data used in the analysis was measured at the centre of the study area and was not specific to a particular subpopulation. However, snowmelt on the west-facing slopes typically was later than the south-facing slopes. Therefore, the LTRE analysis could be refined with localized weather data and snowmelt patterns specific to individual subpopulations or talus patches.

Recent studies of pika abundance and persistence in North America and Asia have reported dramatic population declines, most parsimoniously associated with effects of climate change and variability (McDonald and Brown 1992, Beever 1999, Grayson 2005, Li and Smith 2005). This thesis added to these reports by including the first population viability analysis (PVA) of any member of the Ochotonidae (**Chapter 7**). The demographic dataset used in this analysis is one of only a few datasets for rock-dwelling pikas, and was the only such dataset for *O. collaris*. The PVA presented in this thesis included a range of plausible scenarios, and showed that pikas in the Ruby Range are in peril of extinction within the next 50 years. This analysis was conservative because it did not consider the effects of climate change or hunting.

Chapters 6 and 7 were based on the same dataset and there are two ways in which their conclusions could be further evaluated and strengthened. First, because pika abundance has declined since 1995 (Figure 6-2) , the LTRE analysis (**Chapter 6**) provided the demographic explanation for the decline, but did not necessarily provide insight into demographic mechanisms for an increasing population. If the population recovers to previous levels then the LTRE and PVA analysis should be repeated to incorporate these data to gain a better understanding of changes in population growth and decline. An alternative approach would be to use a fixed-design LTRE similar to that used by Cooch et al. (2001) in which the time series was classified into distinct phases based on food-availability, or periods of increase and decline. Secondly, juvenile survival was calculated for post-dispersal pikas because of 1) inaccessibility of natal nests within talus, and 2) the extremely low capture probability of non-territorial (and therefore non-haying) individuals. Analyses such as the LTRE and PVA would benefit from improved estimates of pika survival during the first year of life. Similarly, litter size at parturition was largely unknown for *O. collaris* because obtaining estimates would likely require captive females or collection of animals to examine uterine scars.

Implications & Projections

The research described in this thesis pointed to climate influences as a dominant driver of pika populations. Continued high-latitude climate warming (Zhang et al. 2000, ACIA 2005) could affect pika populations in several ways. First, the PDO was strongly correlated to adult survival via timing of spring snowmelt. Earlier spring snowmelt was positively correlated to subsequent over-winter survival and later snowmelt should decrease over-winter survival. Second, there is preliminary evidence that freeze-thaw-freeze events during winter are associated with high over-winter mortality at our study site (Smith et al. 2004). Such events are predicted to increase in frequency (IPCC 2001, ACIA 2005) with potentially large negative effects on collared pikas. Third, changes in climate patterns may affect the plant community structure through changes in soil nutrient cycling or length of growing season.

Empirical research at our site demonstrated the strong effects that collared pikas have on above ground biomass, species diversity, plant morphology, and senescence (McIntire and Hik 2002, 2005). Similarly, other experiments at our site showed changes in plant competition intensity (Mitchell 2006), species diversity (D.S. Hik, unpublished data), seasonal phenology (D.S. Hik, unpublished data), and physiology (Tait 2002) as a result of simulated climate change. Therefore, both pikas and climate have important implications for the vegetation community.

Because pikas appeared to make complex inter- and intra-specific decisions regarding the plants cached in their haypiles, a change in the vegetation community, or individual species, could alter the nutritional and energetic composition of the haypile with potential consequences for pika over-winter survival (Figure 8-1). Therefore, the bottom-up influences on the vegetation community through climate change could trigger top-down changes in the vegetation community through altered herbivory patterns.

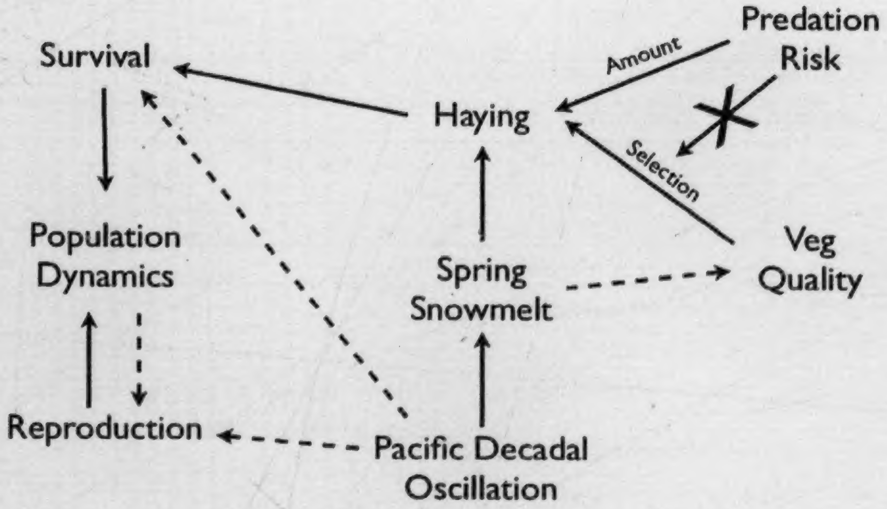
Predation Risk
Survival
Amount
Haying
Selection
Population Dynamics
Spring Snowmelt
Veg Quality
Reproduction
Pacific Decadal Oscillation

Figure 8-1: Interactions of pikas with predation risk, vegetation, and climate as they relate to foraging behaviour and pika population dynamics in southwest Yukon. Solid lines represent relationships examined in this thesis while dotted lines represent proposed relationships and directions for future study. An 'X' drawn through an arrow indicates a hypothesized relationship that was unsupported by data.

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APPENDIX A: DESCRIPTION OF FORAGE SPECIES USED IN CAFETERIA TRIALS

Table A1: Description of six forage species used in cafeteria trials to test hypotheses regarding forage selection by collared pikas (*Ochotona collaris*) in southwest Yukon. Taxonomy and species names followed Cody (2000).

	Artemesia norvegica	*Carex consimilis*	*Dryas octopetala*	*Cassiope tetragona*	*Polygonum bistorta*	*Salix reticulata*
Family	Asteraceae (Compositae)	Cyperaceae	Rosaceae	Ericacae	Polygonaceae	Salicaceae
Description	Erect perennial herb, caespitose growth form, rhizomatous, 10-60 cm stems	Loosely tufted clonal sedge, erect culms 25-40 cm high	Low, mat-forming shrub	Dwarf matted evergreen shrub, up to 30 cm tall	Erect spike, Herbaceous	Prostrate shrub, leaves elliptical
Common Name	'mountain sagewort'	---	'white mountain avens'	'arctic white heather'	---	'net-veined willow'

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APPENDIX B: LIST OF FORAGE SPECIES FOUND IN PIKA HAYPILES

Collared pikas (*Ochotona collaris*) collect and store multiple plant species within their haypiles. Below is a partial list of plant species identified in haypile samples from southwest Yukon. We did not attempt to identify graminoids, mosses, lichens, or infrequently occurring species. Taxonomy followed Cody (2000).

ASTERACEAE
Artemesia norvegica
Petasites frigidus.

CYPERACEAE
Carex consimilis
Carex spp.

ERICACEAE
Cassiope tetragona
Vaccinium uliginosum
Vaccinium vitis-idaea

POLYGONACEAE
Polygonum bistorta
Polygonum viviparum

RANUNCULACEAE
Anemone sp.

ROSACEAE
Dryas octopetala
Potentilla sp.

SALICACEAE
Salix reticulata
Salix arctica
Salix polaris
Salix rotundifolia

SCROPHULARIACEAE
Pedicularis sp.

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APPENDIX C: CALCULATION OF POPULATION GROWTH RATE FROM A 2×2 MATRIX[2]

Given the 2×2 projection matrix **A**,

$$\mathbf{A} = \begin{bmatrix} 0 & F_A \\ P_J & P_A \end{bmatrix}$$

where F_A is adult female fertility, P_J is juvenile female survival, and P_A is adult female survival, the discrete-time population growth rate, λ, can be calculated according to:

$$\lambda = \frac{P_A + \sqrt{P_A^2 + 4P_J F_A}}{2}.$$

For example, the projection matrix **B**,

$$\mathbf{B} = \begin{bmatrix} 0 & 1.2 \\ 0.53 & 0.85 \end{bmatrix}$$

has a discrete-time population growth rate, λ, of 1.329.

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[2] Thank you to Dr. Mark Lewis for suggesting this method.